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Unraveling Ecological Effects on Social Behavior. Insights from Tent-roosting Bats

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UNRAVELING ECOLOGICAL EFFECTS ON SOCIAL BEHAVIOR. INSIGHTS FROM TENT-ROOSTING BATS

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To my mother

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ABSTRACT

Although group living has been associated with high fitness cost, multiple lines of evidence have suggested that it has evolved multiple times independently. Given the wide diversity of social systems, it appears that multiple explanations are necessary to understand this process. Although evidence indicates that multiple ecological and environmental factors might promote variation in cohesion of social organisms, studies investigating how these factors interrelate and shape social structure have been limited.

In the tropics, there are at least 23 bat species that roost in modified structures called tents. These species present a wide diversity in social systems. Moreover, they have divergent evolutionary origins but similar roosting habits, suggesting convergence in roost use. These characteristics make this group an ideal system to test hypotheses regarding effects of ecological and environmental factors in evolution and stability of social groups. Thus, my objectives were first to investigate the importance of habitat factors in predicting presence and density of the tent-roosting bat *Uroderma bilobatum*. Additionally, I wanted to determine relative contributions of habitat factors on group cohesion and stability.

I found that presence of coconut palms (*Cocos nucifera*) had the highest unique predictive power of presence and density of *U. bilobatum*. Additionally, I found that roost characteristics contributed more to the explained variation in group relatedness. This pattern was driven by relatedness of adult females within social groups, suggesting that females using roosts of specific characteristics exhibit higher relatedness. To determine if this pattern holds across multiple tent-roosting bat species, I tested for correlated evolution between group stability and roost lifespan. I found that most bats that used tents of short lifespan also had stable groups, and

most species that used tents of long lifespan had unstable groups, suggesting that group stability and tent lifespan did not evolve independently.

The observed relationships between roosting ecology, group cohesion and stability in tent-roosting bats suggest that roosts play an important role in the evolution of group formation. Incorporating ecological and environmental factors in the study of sociality will allow broad understanding of the forces that bring together individuals into cohesive social groups.

CHAPTER 1: INTRODUCTION

INTRODUCTION

EVOLUTION OF GROUP LIVING.— Group living has always intrigued researchers. At first glance, group living represents an evolutionary puzzle because of the high fitness costs associated with breeding under situations of high density. Some of these costs are increased intensity of competition for resources, cannibalism, infanticide and increased likelihood of disease and parasite transmission (Alexander 1974, Danchin & Wagner 1997). Moreover, group living also increases conspicuousness, making group-living predators less effective and group-living prey more vulnerable (Alexander 1974). Nonetheless, multiple phylogenetic analyses have shown that group living has evolved independently multiple times, implying that individuals must benefit by living with relatives and these benefits at least balance the costs (Danchin & Wagner 1997). Moreover, understanding evolution of group living requires explanation not only of why individuals come together and form social systems, but also why initially loose aggregations turn into highly cohesive and stable societies (Aviles 1999). Before the 1990's, two hypotheses dominated discussion on the evolution of group formation and stability: increased chances of acquisition and protection of resources and predator avoidance (reviewed in Alexander 1974). Nonetheless, to date, multiple lines of evidence have suggested that groups are found even in places where resources are not limited (*e.g.* Rossiter *et al.* 2002). Likewise, many studies have emphasized a negative relationship between predation risk and nearest neighbour distance or colony size, while others have found no relationship or the opposite trend (Møller 1987, Anderson & Hodum 1993). Thus, given the wide diversity and complexity of social systems, it appears that multiple explanations are necessary to explain this phenomenon (Danchin & Wagner 1997, Aviles 1999). However, despite more than 3 decades of research, we still lack a

general framework to organize all the potential routes to group living (Danchin & Wegner 1997).

BATS AND SOCIAL SYSTEMS.— Bats stand out among mammals for the high number of species that are social (McCraken & Wilkinson 2000). The vast majority of species live in groups and their social systems are among the most diverse of all mammals (Bradbury 1977, McCraken & Wilkinson 2000). Moreover, bats exhibit multiple characteristics that are rare in other groups. For example, although bats have small body sizes, they have long life expectancies (Barclay & Harder 2003). Likewise, their ability to fly allows them to disperse long distances; however, many species exhibit strong philopatry (Burland & Wilmer 2001). One of the most intriguing characteristics of bats is that group sizes range over several orders of magnitude and cohesiveness and stability of these groups vary not only among but also within species (McCraken & Wilkinson 2000, Kunz & Lumsden 2003).

In the tropics there are at least 23 bat species that roost in modified structures called tents (Kunz *et al.* 1994, Kunz & Lumsden 2003). Tents are created by cutting the petiole or other plant structures, creating an enclosed space where bats roost (Phillips 1924, Balasingh *et al.* 1993, Balasingh *et al.* 1995, Bhat 1994, Bhat & Kunz 1995). Depending on the phylogeny used for comparison, tent-roosting habits may have evolved 3 to 4 times or disappeared in many clades within the family Phyllostomidae (Kunz *et al.* 1994). Convergence in tent-roosting behavior suggests exposure to similar selective pressures related to foraging and roosting behavior in structurally similar forests (Kunz *et al.* 1994). Moreover, tent-roosting bats exhibit a wide variety of social systems, with cohesiveness varying even within species. Bradbury (1977) and McCraken & Wilkinson (2000) classified these social systems into 3 different groups based on polygyny: (1) seasonal single male-multi-female groups, (2) year-round harems with less stable female composition, and (3) year-round harems with stable female composition. (Alexander

1974). This diversity of characteristics makes bats a highly interesting group to understand causes and consequences of group living.

HABITAT AS A PREDICTOR OF DENSITY AND DISTRIBUTION.— It has been suggested that animal associations with specific areas result from individual choices for breeding sites (Møller 1987, Shields *et al.* 1988, Stamps 1988, Terhune & Brillant 1996). This is because when selecting breeding sites, individuals have to rely on cues that reflect habitat quality (Brown *et al.* 1996). These cues correspond to habitat characteristics and presence of conspecifics with high reproductive fitness (*e.g.* reproductive success; Shields *et al.* 1988, Brown *et al.* 1996, Boulinier *et al*. 1997). Moreover, individuals respond differently to habitat at different scales (Morris 1987). Macrohabitat characteristics such as habitat types (*e.g.* forest type) can define coarse patterns such as presence and density of individuals. On the other hand, microhabitat characteristics encompassing heterogeneity within particular habitats (*e.g.* particular patches of habitat, roost characteristics) can influence important fitness parameters such as cooperation and reproductive success. Therefore, to accurately examine animals' responses to habitat and reach relevant ecological conclusions regarding habitat use, different spatial scales should be considered (Morris 1987, Stapp 1997, Stevens & Tello 2009). Additionally, density of individuals at particular areas determines important parameters of social systems that ultimately influence cohesiveness and stability of social groups. These parameters are adult sex ratios (Hamilton 1967), male and female reproductive tactics (Andersson 1994), variance in reproductive success (Clutton-Brock 1988) and different aspects of parental care (Clutton-Brock 1971). Therefore, disentangling habitat factors influencing density of bats will be essential to understand causes of group living and group cohesion.

Peter's tent-roosting bat (*Uroderma bilobatum*), a medium (c. 17 g) phyllostomid tent-rooster is known to form highly gregarious groups varying from 1 to 59 individuals (Baker &

Clark 1987, LaVal & Rodríguez-Herrera 2002). This tent-roosting bat is usually found in a wide variety of forested and human-modified habitats (LaVal & Rodríguez-Herrera 2002) and its group size and composition vary depending on habitat (Sagot *et al.* submitted). Therefore, this species represents an ideal case to study density and behavioral plasticity responses to habitat and environmental variation. Thus, in Chapter 2 (Sagot *et al*. submitted), I determine the importance of habitat factors in predicting not only presence but also density of *U. bilobatum*. I study which habitat characteristics better predict presence, density and distribution within two habitat scales (macrohabitat and microhabitat). Moreover, I determine the relative contribution of these two scales in predicting areas with high density of bats. Although *U. bilobatum* is a widely distributed species, to my knowledge, this is the first study that presents a detailed description of habitat preference at different spatial scales and how this may have affected distribution and density of this Neotropical bat. Identifying habitat characteristics that influence variation in density will be important in disentangling relationships between habitat and group living.

HABITAT AND THE STRENGTH OF SOCIAL INTERACTIONS.— Although social systems were once believed to be fixed species attributes, multiple lines of evidence now suggest that species are socially flexible in response to spatial and environmental variation (Lott 1984, 1991, Slobodchikoff 1984, 1988, Slobodchikoff & Schulz 1988, Travis *et al.* 1995). Multiple ecological factors have been suggested to influence cohesion of social organisms such as constraints on breeding (Emlen 1991), predator pressure (Alexander 1974, Wilson 1975, Caraco & Pulliam 1984, Stern & Foster 1996), intra and interspecific competition (Wilson 1975, Buss 1981, Hogendoorn & Velthuis 1993) and unpredictable environments (*e.g.* Emlen & Wrege 1991, Jarvis *et al.* 1994). Furthermore, environmental factors (Christiansen & Reyer 2011, Zachos & Hartl 2011) are known to be important

determinants of social structure (Bronikowski & Altmann 1996, Pusey & Packer 1997). Thus, differences in adaptative adjustment of males and females to these ecological and environmental factors throughout their range should promote variation in group cohesion (Rubenstein 1980, Dunbar 1981, Chaverri & Kunz 2010, Campbell 2010). Nonetheless, studies investigating how these factors interrelate and shape social structure have been limited. In Chapter 3, I describe genetic structure, degrees of inbreeding and patterns of natal dispersal in the Peter's tent-roosting bat, *U. bilobatum* at three different levels (group, locality and region). Moreover, I determine relative contributions of different habitat factors at 3 different scales (roost, structural and macrohabitat) on group cohesion and stability. This study provides important information on the ecological and microevolutionary patterns affecting cohesion and stability of social structure.

ROOSTING ECOLOGY AND THE EVOLUTION OF GROUP STABILITY.— Diurnal roosts are among the most important places for social interactions in bats (Wilkinson 1986, Zahn & Dippel 1997, Fleming *et al.* 1998, Kunz & Hood 2000, Kerth *et al*. 2003, Keeley & Keeley 2004, Chaverri & Kunz 2006, Ortega & Maldonado 2006). This is because they provide protection for predators and inclement weather (Ferrara & Leberg 2005, Lausen & Barclay 2006). Moreover, roosts can be relatively scarce, at least in some habitats and costly to construct (Kunz 1982, Kunz & Lumsden 2003, Kalko *et al.* 2006, Rodríguez-Herrera *et al.* 2007). Thus, because roosts have significant influence on fitness and survival in bats, it is reasonable to assume that they are the most important elements of social interactions in many bat species (Chaverri & Kunz 2010). Although only few studies have addressed this issue, some trends can be observed among species using different roost types. For example, roost abundance plays an important role in group stability and cohesion. Bats roosting in abundant structures such as rock crevices and tree

cavities, frequently switch roosts and group partners (Brigham 1989, Kerth & König 1999, Lausen & Barclay 2002, Willis & Brigham 2004, Garroway & Broders 2007, Popa-Lisseanu *et al.* 2008). In contrast, some species using less abundant roosts exhibit higher levels of social cohesion (McCracken & Bradbury 1981, Wilkinson 1985, Lewis 1995, Brooke 1997). Nonetheless, although more than half of the approximately 1100 species of bats use plants exclusively or opportunistically as roosts (Kunz & Lumsden 2003), to date there is no comparative study that links their roosting ecology with group cohesion and stability. Within foliage roosting bats, tent-roosters stand out because they actually modify natural structures to construct their own roosts. Thus, different ecological and evolutionary pressures might affect tent-roosting bats. For example, their ability to construct roosts facilitates flexibility in choices of roost structures. On the other hand, tent-roosting bats have greater exposure to predators such as snakes, raptors and monkeys (Boinski & Timm 1985) relative to bats that utilize preexisting and more permanent refuges. Additionally, these species may benefit from group living because members can cooperate in roost construction (Rodríguez-Herrera *et al.* 2008, Alcock 2009). In Chapter 4 (Sagot & Stevens 2012), I conducted a literature review on tent-roosting bats, to collect information on social systems and tent lifespan. I tested for correlated evolution of group stability and group longevity with tent lifespan. The goal was to better understand effects that roosts have on social bonds of tent-roosting bats. The ability to identify how roost lifespan can interact with other ecological processes to produce complex behaviors provides the basis for understanding the variety of mechanisms that interact to produce the diversity of social systems in bats.

Finally, in Chapter 5, I summarize and discuss insights gained in Chapter 2 with the study of density response and distribution of bats based on habitat characteristics and its implications

to evolution and plasticity in social groups. Moreover, I review the habitat effects on the genetic structure and inbreeding patterns in *U. bilobatum,* investigated in Chapter 3. Lastly, I examine the comparative approach between roost lifespan and group cohesion in tent-roosting bats from Chapter 4 and provide conclusions and insights from these results.

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CHAPTER 2. MACRO AND MICROHABITAT ASSOCIATIONS OF THE PETER'S TENT-ROOSTING BAT (*URODERMA BILOBATUM*): HUMAN INDUCED SELECTION AND COLONIZATION?

INTRODUCTION

Human-induced habitat alterations are ubiquitous. The vast distribution of mosaic landscapes consisting of configurations of intact and human-altered vegetation has forced species to inhabit novel environments worldwide (Graham 2001, McGarigal & Cushman 2002, Knowlton & Graham 2010). However, little is known about the effect of these rapid changes on natural populations (Wiens *et al.* 1993, Diffendorfer *et al.* 1995, Ims 1995). As a result, understanding habitat selection under contemporary scenarios, and especially how novel landscapes affect population dynamics will inform a wide variety of ecological, evolutionary and conservation-related questions (Dunning *et al.* 1992, McRae *et al.* 2008, Knowlton & Graham 2010).

To detect organismal responses to altered landscapes, studies must be broad enough in spatial extent to incorporate multiple areas of suitable and unsuitable habitat (Hanski 1994). Although species-specific habitat preferences are widely known, such large scale studies often preclude detailed investigation of individual behavior or population level demographics that are also major influences on population level patterns of habitat selection. Including such preferences that are associated with specific behavioral, morphological, and physiological adaptations may enhance understanding of how organisms improve fitness and success in particular habitats (Morris 1987). Moreover, animal populations can respond to habitat in both a coarse- and fine-grained fashion (Morris 1987). Coarse-grained characteristics can be defined by macrohabitat and are typified by broad, discrete habitat types (*e.g.* forest type, land use category) that vary at landscape scales. Fine-grained characteristics encompass heterogeneity within a particular habitat and are often defined by microhabitat characteristics (*e.g.* particular patches of

habitat, roost characteristics). To accurately examine habitat responses and reach relevant ecological conclusions regarding habitat use, different spatial scales should be considered (Morris 1987, Stapp 1997, Stevens & Tello 2009). Information on relevant scales can be used to study population dynamics and fitness and to propose education, management, and conservation strategies that merge human needs and ecosystem requirements of organisms.

Peter's tent-roosting bat (*Uroderma bilobatum*) represents an ideal species to explore response to human-modified habitats, as well as importance of incorporating different spatial scales while investigating habitat selection. *U. bilobatum* is one of the largest and more gregarious tent-roosting bats (those capable of constructing roosts called tents) with groups varying from 1 to 59 individuals, consisting mostly of females and their dependent young (Baker & Clark 1987, Sagot pers. obs.). This fruit eating bat is a keystone species in tropical forests, as it promotes plant community diversity and secondary succession (Fleming & Heithaus 1981, Fleming 1988, Gorchov *et al.* 1993) especially in small and medium-sized forest fragments. Prior observations indicate that *U. bilobatum* is becoming more abundant in human-altered habitats, and may prefer to roost in a number of introduced plant species (Timm & Lewis 1991, Lewis 1992, LaVal & Rodríguez-Herrera 2002, Sagot pers. obs.). *U. bilobatum* might respond distinctly to differences in abundance and distribution of plants in forest and human-modified areas. Thus we should expect differences in population density across different habitats. These differences in density can have consequences on population growth and resilience to disturbances due to variation in reproductive success and sex ratios (Caro 1998). Changes in population dynamics of this important seed disperser due to differential roosting habits both in forests and human-modified habitats might have detrimental consequences to persistence of small forest fragments. Therefore, if humans facilitate use of non-native habitats, it is important to understand how this

process might affect the roosting ecology of Peter's tent-roosting bats. *U. bilobatum* has not received much attention from a conservation perspective despite its large geographic distribution. Studies determining response to habitat across a range of spatial perspectives remain little explored.

The aim of this study is to investigate what habitat characteristics influence presence, density and distribution of *U. bilobatum*. My objectives are: (1) to identify possible predictors of *U. bilobatum* distribution at the local level; (2) to determine which scale (macrohabitat or microhabitat) best predicts *U. bilobatum* habitat selection; and (3) to determine whether we can use presence and density of tents instead of bats as a useful surrogate of habitat selection.

MATERIALS AND METHODS

STUDY SITE AND SAMPLING.— Fieldwork was conducted at two areas in Costa Rica between June 2007 and May 2009. Areas were selected because of different climate, vegetation and anthropogenic influences. The Central Volcanic Cordillera separates both areas and is an important biogeographic barrier in Costa Rica (Janzen 1983). The first site is Sarapiquí, located in Heredia province, on the Caribbean versant (10°23'55.88" N, 84°08'06.23" W; Fig. 2.1). Elevation ranges from 37 to 187 m asl (see Sanford *et al.* 1984 for a more detailed description). Carara occurs in Puntarenas province, in the Central Pacific region of the country (9°44'55.78" N, 84°37'1.29" W; Fig. 2.1) (see Boza & Cevo 1998 for a more detailed description).

To assess abundance and distribution of *U. bilobatum* in Sarapiquí and Carara, I visited all plant species known to be used as roosts that were present in the study area (*Cocos nucifera*, *Attalea rostrata*, *Musa acuminata*, *Cryosophila guarara*, *Carludovica.* spp. and *Heliconia* spp.; Kunz & Lumsden 2003, Rodríguez-Herrera *et al.* 2007).

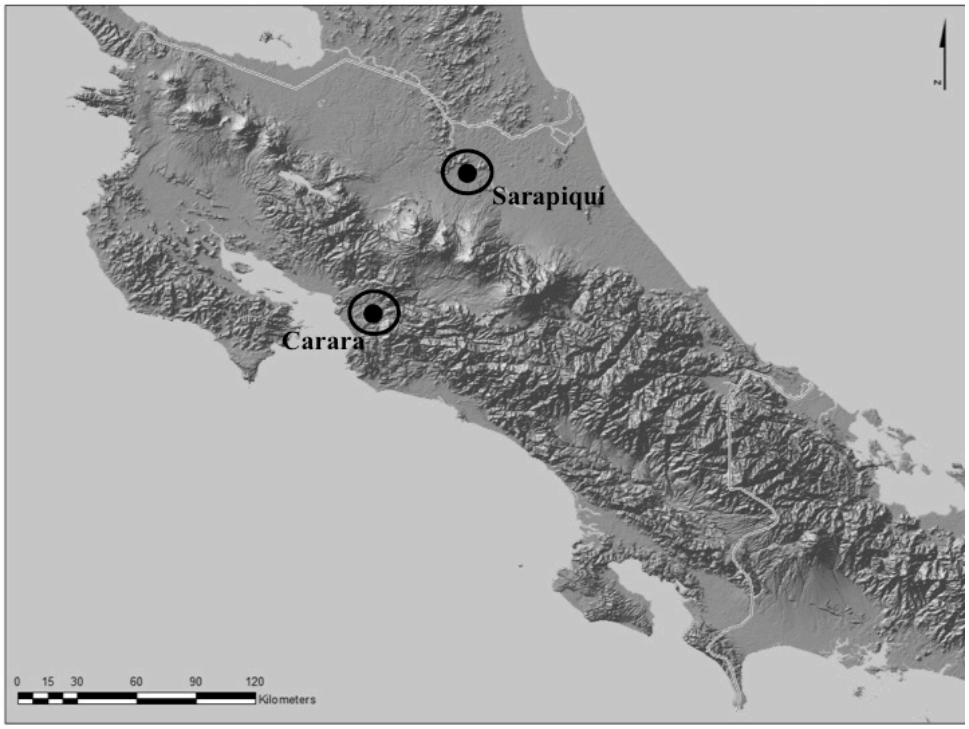

FIGURE 2.1. Field sites in Costa Rica.

Tents are conspicuous structures and can be observed from long distances. Moreover, *U. bilobatum* is the only tent-roosting bat known to construct tents in coconut palm (*Cocos nucifera*) and the palm (*Attalea rostrata*) (Kunz & Lumsden 2003). Therefore, all tents found in these two palm species were assumed to be built by *U. bilobatum*. Tents made in banana plants (*Musa acuminata*), guarara palms (*Cryosophila guarara*), hat palms (*Carludovica.* spp.) and heliconias (*Heliconia* spp.) can be used by other tent-roosting bats (Rodríguez-Herrera *et al.* 2007). Nonetheless, those made by *U. bilobatum* can be distinguished by the size and configuration of cuts made in the leaf which are longer and less consistent than those made by other species. I searched for bats and tents in good condition in forested and human-modified habitats, covering approximately the same area in both types of habitat (area determined on a georeferenced map in ArcGIS 9.3.2; ESRI 2009). Tents were considered in good condition when

there was no sign of deterioration or physical damage, such as lack of leaflets or severe necrosis. In the forest, I followed available trails and randomly located 10 2-km transects per site. Spatial locations of random transects were selected from a georeferenced map of the area in ArcGIS 9.3.1 (ESRI 2009). Human-modified areas were defined as plantations, grassland or urbanized sites. In these areas I followed available streets and roads, covering approximately the same distance covered in the forest (distance determined on a georeferenced map in ArcGIS 9.3.2; ESRI 2009). To ensure similar effort at both sites, I searched for plants and tents that were located within 100 m from trails and roads. Numbers of bats were determined by observation. If tents were high, binoculars were used. For every plant visited, I recorded its geographic location (geographic coordinates), number of tents and number of bats.

I estimated influence of two different spatial scales and the relative contribution of different variables within these scales on presence and density of bats and tents of *U. bilobatum*. I used the random number generator function in Microsoft Excel, to select 100 plants with tents (including all plants where bats were found) and 100 plants without tents per habitat (forest and human-modified in Carara. In Sarapiquí, no bats were found in the forest. Thus, data from this place consisted in 112 tents (including tents where bats were found) and 288 plants without tents. This was to obtain a balanced number of plants (total n = 800) because I found more plants used to build tents in human-modified areas than in the forest, and more in Carara than Sarapiquí. From plants selected, I measured habitat corresponding to macrohabitat and microhabitat scales. Macrohabitat was defined as discrete habitats in the landscape based on land use (human-modified/ forest), site (Carara vs Sarapiquí) and distance to the forest (measured from a georeferenced map of the areas in ArcGIS 9.3.1; ESRI 2009). Microhabitat was defined as particular habitat subsets within the macrohabitat. Microhabitat characteristics were measured in

a 20 m diameter plot around the 800 plants selected for analyses. Variables measured were: amount of herbaceous cover, number of bushes (woody plants with a DBH less than 20 cm), number of trees (woody plants with a DBH larger than 20 cm), average tree diameter at breast height (DBH), tent height, plant height, plant species (represented by dummy variables in analyses; Suits 1957) and average light penetration measured with a quantum light meter (Hydrofarm West, model 2053), taken at cardinal points. Density of bats was determined as the number of individuals divided by the area of the 20 m diameter plot (bats/ 314 m^2) and since plants can have multiple tents, tent density was defined as the number of tents per plot (tents/ 314 m^2).

ANALYTICAL METHODS.— Macrohabitat scale. To predict bat or tent presence based on macrohabitat, I performed two separate stepwise multiple logistic regressions (Crawley 2007). I removed from the model the non-significant and collinear variables using a model selection under the stepwise AIC procedure implemented in the package bootstepAIC (Venables & Ripley 2002, Austin & Tu 2004; R version 2.10, R Development Core Team 2009). This test uses a bootstrap procedure (1000 bootstrap samples) to return the variables that significantly contribute to the model (Venables & Ripley 2002, Austin & Tu 2004). The procedure simulates a new dataset by subsampling with replacement, then refitting the model using the new dataset and running the stepAIC algorithm. After 1000 iterations, I tallied how many times each variable was selected. Only variables selected in 100% of the iterations were included in the analyses (Venables & Ripley 2002, Austin & Tu 2004; R version 2.10, R Development Core Team 2009).

To determine effects of distance to forest, site and land use on density of bats or tents, I conducted two separate analyses of covariance (ANCOVA) where density of bats or tents was

the response variable, site and land use were two categorical explanatory variables and distance to forest was a continuous covariate. I removed from the model the non-significant variables using the function "step" from the package Stats (R version 2.10, R Development Core Team 2009), which tests all terms to see whether they are needed in the minimal adequate model. The criterion used was AIC (Crawley 2007). Because in this case I was only interested in using macrohabitat (site, habitat and distance from the forest) to predict higher densities of bats or tents, this analysis was conducted only for plots where I found both bats and tents. Analyses were conducted in R (version 2.10, R Development Core Team 2009).

Microhabitat scale. To determine ability to predict presence/absence of bats or tents based on microhabitat, I again performed a stepwise multiple logistic regression (Crawley 2007) where presence/absence of bats or tents were used as response variables and microhabitat characteristics were predictor variables. I report the Beta coefficients that represent standardized coefficients of the regression. I also performed the model selection procedure as described in the macrohabitat scale analyses and repeated regressions with variables selected by this procedure. I used Poisson regression to predict variation in density of bats and tents based on microhabitat because residuals were not normally distributed. Since in this case I was interested in higher densities of bats or tents based on microhabitat scale variables, Poisson regression was performed only for plots where I found both bats or tents. Beta coefficients are also reported for these regressions. Analyses were conducted in R (version 2.10, R Development Core Team 2009).

Relative predictive abilities of different scales. In order to determine relative ability of each habitat perspective to predict presence/absence and density of bats or tents, I performed variation partitioning based on redundancy analysis (RDA; Legendre & Legendre 1998). I was interested

in unique variation explained by a particular scale (*e.g.* macrohabitat or microhabitat) after controlling for the other scale. In order to obtain the relative ability of each habitat component to predict high densities of bats or tents, I selected only plots where I found both bats and tents. Moreover, since microhabitat analyses revealed that roost characteristics contributed more to the explained variation, I subdivided microhabitat scale into two different components: (1) structural, characterized by variables describing the area surrounding the roosts (amount of herbaceous cover, number of bushes, number of trees, and average DBH) and (2) roost, characterized by variables describing roost characteristics (tent height, plant height, plant species). By subdividing microhabitat, my goal was to ascertain the importance of roosts compared to other microhabitat variables in predicting presence and density of *U. bilobatum*. Variables were standardized for the analysis using the function "standardize" from the package "dse"1 in R (version 2.10, R Development Core team 2009), which rescales numeric variables to have a mean of 0 and standard deviation (sd) of 0.5, so that the scaled regression coefficient corresponds to a change from mean -1*sd to a mean +1*sd. Binary variables are rescaled to have a mean of 0 and a difference of 1 between their categories. Variation partitioning analysis was conducted in VarCan (version 1, Peres-Neto *et al.* 2006).

RESULTS

A total of 7597 individual plants used as roosts by *U. bilobatum* were sampled at both study sites. I found tents in 10% of sampled plants (n = 764) corresponding to 6 different species (Table 2.1; Table A.1). These 764 plants contained a total of 1606 tents, out of which only 14% (n = 228) were occupied (Table 2.1; Fig. 2.2). Habitat information was available for 107 out of

the 228 occupied tents. At both sites combined, I found a total of 588 bats occupying 228 tents. The median group size per tent was 2 (range 1 to 58).

MACROHABITAT SCALE: PREDICTING PRESENCE AND DENSITY OF BATS AND TENTS.— Bats. Regression indicated differences among plots regarding bat presence or absence based on land use, site and distance to the forest; however, explained variance was low ($R^2 = 0.020$; *d.f.* = 245; $P < 0.001$). Overall, plots containing bats were more numerous in human-modified habitats of Carara. No plots containing bats were found in the forest of Sarapiquí. Moreover, higher densities of bats were found at Carara (0.900 ± 3.000 ind/plot in Carara vs. 0.420 ± 1.300 ind/plot in Sarapiquí; Fig. 2.2A). There were no significant differences in density of bats at different distances to the forest nor between forest and human-modified areas ($R^2 = 0.110$; $F_{1,103} = 5.092$; $P = 0.002$). Interactions between site, distance to the forest and land use were not significant.

TABLE 2.1. Number of plants, number of tents and number of bats, of the species *U. bilobatum* found after sampling similar areas (determined by a georeferenced map on ArcGIS v9.3), at two different habitat types (forest and human-modified) in Carara National Park and surrounding areas on the Pacific slope, and Sarapiquí in the Caribbean slopes of Costa Rica.

Site	Habitat type	Number of plants	Number of tents	Number of bats	Plant taxa
Carara	Human-modified	1828	543	336	*Attalea rostrata, Carludovica* sp.,
	Forest	1944	232	28	*Cocos nucifera, Cryosophila guarara, Heliconia* sp., *Musa acuminata*
Sarapiquí	Human-modified	3355	801	224	*Carludovica* sp., *C. nucifera, Heliconia*
	Forest	470	30	0	sp., *M. acuminata,*

Tents. Logistic regression indicated that tents are not distributed randomly among land use categories, site and distance to the forest; however, explained variance was low ($R^2 = 0.020$*; d.f.* = 796; $P = 0.003$). ANCOVA indicated that there was an effect of site on tent density but it depended on distance to the forest (10.1 tent/km^2 in Carara and 13 tent/km^2 in Sarapiquí; $R^2 = 0.050$*;* $F_{3,307} = 5.091$; $P = 0.006$; Fig. 2.2B).

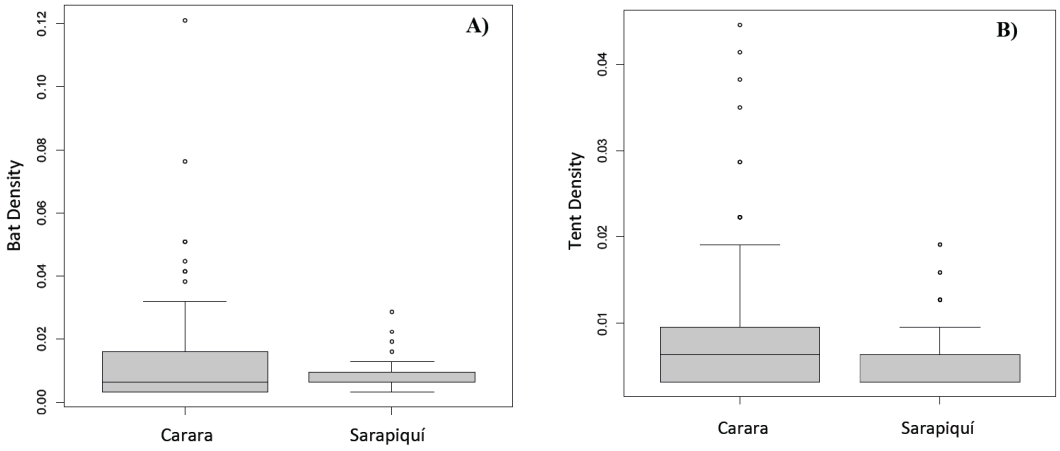

FIGURE 2.2. Mean and standard deviation of **(A)** bat density and **(B)** tent density between Carara and Sarapiquí.

MICROHABITAT SCALE: PREDICTING PRESENCE-ABSENCE AND DENSITY OF BATS AND TENTS.

— Bats. Microhabitat characteristics explained 22% of variation in presence/absence of bats (*d.f.* = 245; $P < 0.001$). For both sites, areas with more bats contained higher numbers of coconut palm, *C. nucifera* (*Beta coeff.* = 3.710; $P < 0.001$) for tent construction that ranged in heights from 8-15 m (*Beta coeff.* = 0.342; $P < 0.001$; Fig. 2.3A) and possess many tents with heights between 5-10 m (*Beta coeff.* = -0.153; $P < 0.001$; Fig. 2.3B). Tree diameter also contributed significantly to explained variation (*Beta coeff.* = 0.0017; $P = 0.001$). Microhabitat characteristics explained 14% of the variation in density of bats (*d.f.* = 106; $P < 0.001$). At both study sites, higher densities of bats were found in habitats with higher numbers of coconut palm,

C. nucifera (*Beta coeff.* = 0.600; $P < 0.001$) with heights that ranged from 8-15 m (*Beta coeff.* = 0.103; $P = 0.003$) and tents with heights ranging from 5 to 10 m (*Beta coeff.* = 0.0043; $P = 0.05$), fewer trees of large diameter (*Beta coeff.* = -0.010, $P = 0.003$), few bushes (*Beta coeff.* = 0.021; $P = 0.009$) and abundant light penetration (*Beta coeff.* = -0.001; $P < 0.001$).

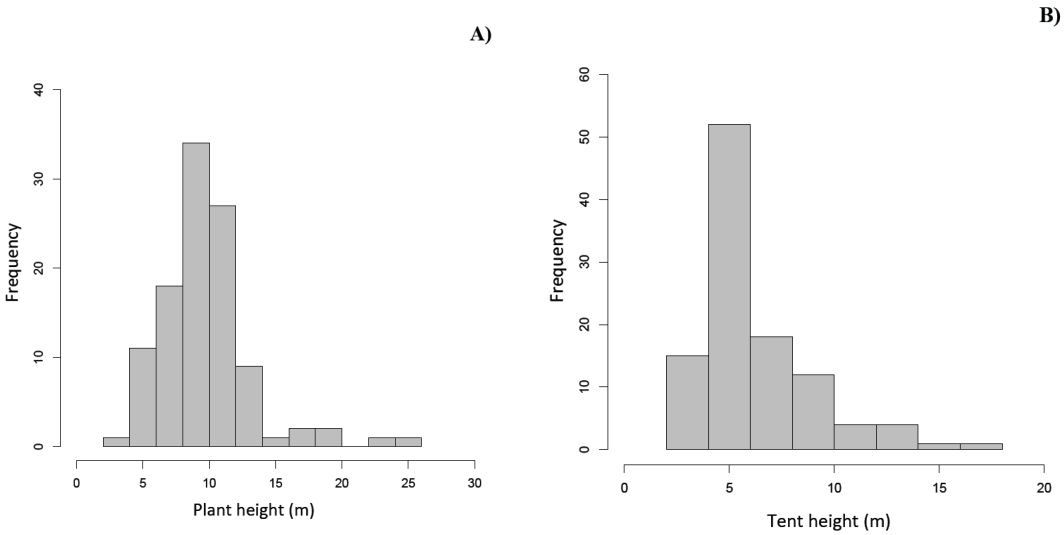

FIGURE 2.3. Histograms representing the most common: **(A)** plant height (m) in plots with presence of bats; **(B)** tent height (m) in plots with presence of bats.

Tents. Microhabitat characteristics explained 87% of the variation in presence/absence of tents ($R^2 = 0.870$; *d.f.* = 796; $P < 0.001$). Presence of tents was associated with plants with heights that ranged from 8-15 m (*Beta coeff.* = -0.451; $P < 0.001$), tents with heights that ranged from 5-10 m *(Beta coeff.* = 1.948; $P < 0.001$) and few or no bushes (*Beta coeff.* = -0.014; $P < 0.001$). Microhabitat variables explained 20% of the variation in density of tents ($R^2 = 0.200$; *d.f.* = 310; $P < 0.001$) Higher densities of tents were associated with presence of *C. nucifera* (*Beta coeff.* = 0.255; $P < 0.001$), *C. guaguara* (*Beta coeff.* = 0.723; $P < 0.001$) and *Carludovica* sp. (*Beta coeff.* = -0.612; $P < 0.001$). Higher density was also associated to habitats with few or no bushes (*Beta coeff.* = -0.002; $P < 0.001$).

RELATIVE IMPORTANCE OF SCALES IN PREDICTING PRESENCE AND DENSITY OF BATS AND TENTS.— Bats. Microhabitat and macrohabitat variables combined explained 22% of the variation among sites in terms of presence/absence of bats ($P < 0.001$; Fig. 2.4A). Microhabitat accounted for more unique variation (11%) than macrohabitat (5%) with 6% jointly accounted for by both sets of variables.

Micro and macrohabitat combined explained 23% of the variation among sites in terms of bat density ($P = 0.030$; Fig. 2.4B). Macrohabitat accounted for more unique variation (13%) than did microhabitat (10%).

Tents. Micro and macrohabitat combined accounted for 64% of the variation in presence/absence of tents ($P = 0.001$, Fig. 2.3C). Microhabitat accounted for 62% of unique explained variance while macrohabitat explained 1%.

Micro and macrohabitat combined accounted for 21% of the variation in density of tents ($P = 0.001$; Fig. 2.4D). Microhabitat had the highest predictive power in explaining tent density (18% of unique variation), while macrohabitat explained 2% of unique variation.

RELATIVE CONTRIBUTION OF ROOST, STRUCTURAL AND MACROHABITAT COMPONENTS.— Bats. All three components (macrohabitat, structural and roosts) combined explained 22% of the variation among sites in terms of presence/absence of bats ($P < 0.001$; Fig. 2.5A). From this explained variation, roost characteristics had the highest predictive power (11% unique variation). Macrohabitat explained 8% of unique variation. Structural characteristics accounted for 1% of unique variation.

All three components combined explained 23% of the variation among sites in terms of bat density ($P = 0.030$; Fig. 2.5B).

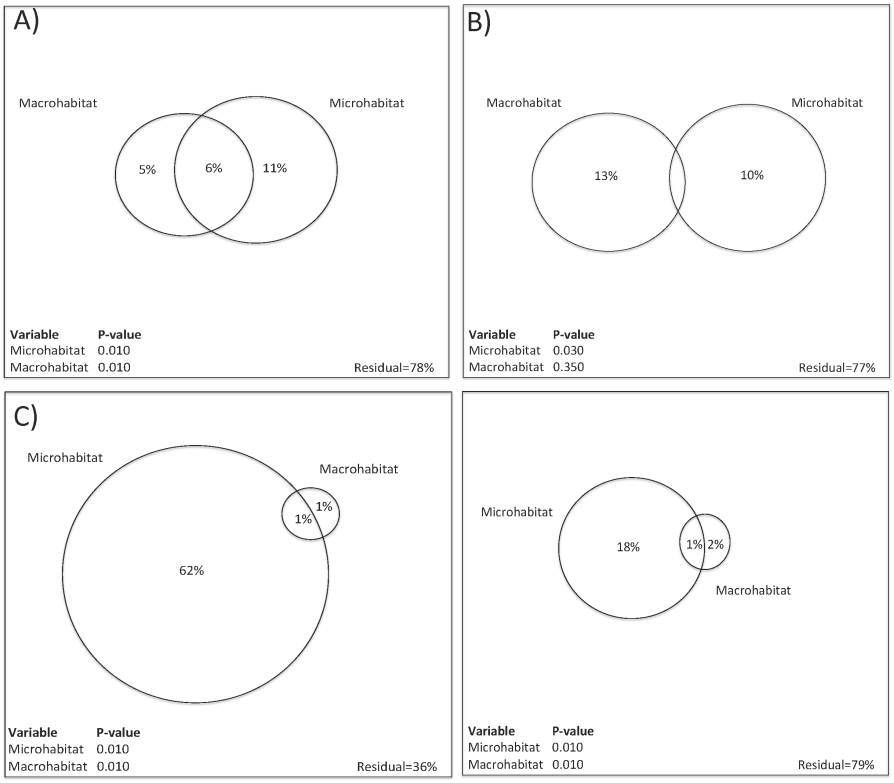

FIGURE 2.4. Variation partitioning analysis to predict: **(A)** presence/absence of bats; **(B)** density of bats; **(C)** presence/absence of tents and **(D)** density of tents, based on microhabitat and macrohabitat scale. Each box represents 100% of the variation. The summed areas of the 2 circles represent the overall variance explained. The area of the circles that is not overlapping represents the variance explained by each individual habitat scale. The area where circles overlap represents variance explained by the interaction of micro and macrohabitat. Explained variances less than 1% are not reported.

Macrohabitat accounted for most of the explained unique variation (13%). The roost component accounted for 7%, and structural component 3%.

Tents. The three components combined accounted for 63% of the variation for presence/absence of tents ($P = 0.001$, Fig. 2.5C). Only the roost component accounted for significant unique variance (60%).

The three components combined accounted 19% of the variation for density of tents ($P = 0.001$; Fig. 2.5D). Roost component had the highest unique predictive power in explaining tent

density (13%). Structural accounted for 2%, while macrohabitat explained only 1% of unique variation in density of tents.

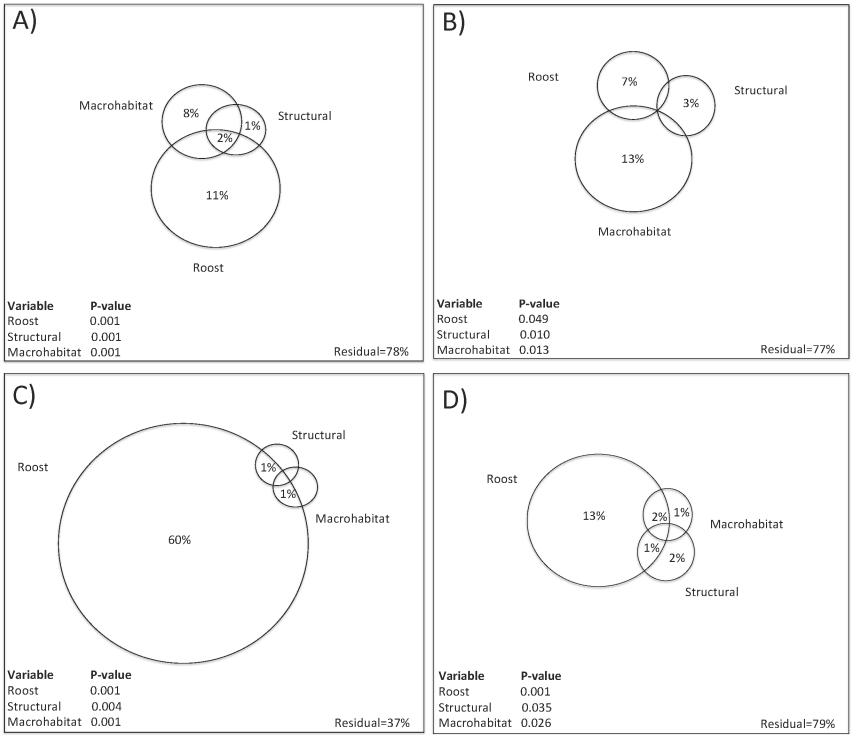

FIGURE 2.5. Variation partitioning analysis to predict: **(A)** presence/absence of bats; **(B)** density of bats; **(C)** presence/absence of tents and **(D)** density of tents, based on structural, roost and macrohabitat components for both sites. Each box represents 100% of the variation. The summed areas of the 3 circles represents the overall variance explained. The area of any circle that is not overlapping any other represents the variance explained by each individual habitat component. The area of any 2 overlapping circles represents variance explained by the interaction of 2 habitat components. The area where the 3 circles overlap represents the variance explained by the interaction of the 3 habitat components. Explained variances less than 1% are not reported.

DISCUSSION

At Carara, *U. bilobatum* was more common in human-modified areas where introduced coconut palms (*C. nucifera*) are more abundant, and was less common inside the forest, where it uses native species, namely guagara palm (*C. guaguara*) and the palm (*A. rostrata*). At Sarapiquí, *U. bilobatum* is also more common in human-modified areas, again, corresponding with higher

density of *C. nucifera.* Moreover, it was absent inside the forest where plants such as *A. rostrata* and *C. guaguara* are rare or nonexistent. After dividing the microhabitat scale into structural and roost components, I found that characteristics of the structural component were poor predictors of presence and density of *U. bilobatum*; however, characteristics of the roost component (plant height, tent height, plant species) have the greatest ability to predict presence and density of tents. There is usually substantial variation in natural environments and correlations that are only low or moderate are not uncommon in ecological work (Hill & Lewicki 2007). Despite substantial variation, it is important to highlight that I was able to explain a substantial amount of the variation in presence and density of bats and tents. Although some of the R^2 found were low, patterns in habitat use by *U. bilobatum* emerged, indicating that habitat characteristics influence distribution of bats and tents.

TENTS VERSUS BATS AS PREDICTORS OF HABITAT SELECTION.— Macro and microhabitat scales were better predictors of tent presence and density than bat presence and density (Fig. 2.3). The fact that I could only predict small amounts of variation in bat presence or density is likely related to a smaller bat sample size compared to tent sample size. Nonetheless, *U. bilobatum* is an obligate tent-roosting bat (Baker & Clark 1987, Timm & Lewis 1992, Kunz & Lumsden 2003, LaVal & Rodríguez-Herrera 2002, Rodríguez-Herrera *et al.* 2007). Thus presence of tents reflects presence of bats. Moreover, although tent-roosting bats that occupy tents of short lifespan, such as *Ectophylla alba,* build and inhabit one tent at a time (Rodríguez-Herrera *et al.* 2008), species that build tents of long lifespan, as is the case of *U. bilobatum* and *Dermanura watsoni* are known to build and utilize multiple tents for short periods of time (Lewis 1992, Storz *et al.* 2000, Kunz & Lumsden 2003, Campbell 2008, Chaverri & Kunz 2006; Sagot

& Stevens 2012). Some bats switch between tents on a weekly or even daily basis (Lewis 1992). This nomadic behavior is more common in tent makers that use long lasting tents (Sagot & Stevens 2012). Because of this, it is not uncommon to find empty tents that were occupied the day before and vice versa. This nomadic behavior makes it more difficult to predict presence of bats based only on the presence of bats. Moreover, since refuges are one of the most important factors impacting bat survival and fitness (Kunz & Lumsden 2003), the mere presence of tents can be considered a good predictor of habitat use by *U. bilobatum*. Because these tents are ephemeral, presence of tents in good condition reflects recent habitat use.

IMPORTANCE OF SCALE IN HABITAT SELECTION.— Organisms can respond to their environments at multiple scales (Morris 1987). Associations at one habitat scale may influence and constrain relationships at broader or finer scales; however, investigators addressing habitat selection have often conducted their studies at single and frequently quite different scales (Wiens 1989, Orians & Wittenberger 1991, Gorrensen *et al.* 2005). Not surprisingly, failure to appreciate scaling differences among organisms has lead to mixed results and disagreement.

Because roost sites are such a critical resource to which most bats are committed to for long periods of time, roosts characteristics (*i.e.* roost component) may often be important determinants of habitat selection (Orians & Wittengerger 1991). Individuals can travel long distances from a safe roost to foraging sites and many species fail to reproduce if adequate roosts are not available even if food supplies are abundant (Orians & Wittengerger 1991). Thus, it is not surprising that roosting habits influence local and global distribution, population density, foraging and mating strategies, social structure and seasonal movements (*e.g.* Altringham 1996, Vonhof & Barclay 1996, Fenton 1997, Kunz & Lumsden 2003). This pattern has been observed

in multiple species including bats that inhabit diverse habitats (*e.g.* Miles *et al.* 2006, Neubaum *et al.* 2007, Rodríguez-Herrera *et al.* 2008, Spada *et al.* 2008, Boland *et al.* 2009, Napal *et al.* 2009) and *U. bilobatum* is no exception. By investigating habitat associations from macrohabitat and microhabitat scales I found that microhabitat (specifically roost characteristics) often is the most important level when selecting habitat. Moreover, the macrohabitat scale, which reflects distribution of plants for tent construction, also was an important characteristic influencing habitat selection.

U. bilobatum was found roosting in 6 different plant species (Fig. A.1). Based on leaf morphology, tent architectures found in these plants were palmate (*C. guaguara* and *Carludovica* spp.), pinnate (*A. rostrata* and *C. nucifera*) and inverted boat (*Heliconia* spp. and *M. acuminata*) (Kunz *et al.* 1994). The fact that *U. bilobatum* preferentially selects plants with very specific leaf morphologies and heights (Kunz & Lumsden 2003) suggests that this bat uses a specific search image to recognize leaves and construct tents in these particular plants independently of the higher taxon that the plant comes from. This becomes evident when searching for plants used for tent construction that are found exclusively in the forest (*A. rostrata* and *C. guaguara*). These plants are morphologically similar to those found exclusively in human-modified areas (*C. nucifera* and *M. acuminate*; Fig. A1) but are not closely related taxonomically. If tent-roosting bat species construct tents only in specific plant species, it is reasonable to assume that distribution and habitat use by tent-roosting bats would be influenced by distribution of these plant species. Although abundances of bats and tents are higher in human-modified areas, *U. bilobatum* is not found far from forest patches (Baker & Clark 1987). Thus, I hypothesize that roosting in plants in human-modified areas, especially coconut palms (*C. nucifera*), reduces time and energy spent looking for plants in which to build new tents and allows use of multiple active

tents in close proximity. Moreover, higher abundances of these plants, compared to native plants used in the forest, and similarities in their morphologies, can also facilitate finding suitable roosts. Additionally, arboreal animals such as squirrels and capuchin monkeys, as well as volant birds of prey, such as the double-toothed kites constitute a significant source of mortality for tent-roosting bats (Boinski & Timm 1985, Souza *et al.* 1997). Therefore, utilizing roosts that are outside the forest might provide a relief from the most common predators. Further investigation is needed to verify this point.

HABITAT COLONIZATION AND HUMAN-INDUCED EXPANSION IN *U. BILOBATUM*. — *Attalea* spp., one of the most commonly used native plants by *U. bilobatum,* originated in South America (east of the Andes) and expanded to Amazonas, the West Indies and Central America (Meerow *et al.* 2009; biodiversity occurrence data accessed through GBIF Data Portal, data.gbif.org, 2010-09-06; Appendix A). Likewise, Hoffmann *et al.* (2003) suggested that lineages of *U. bilobatum* last shared a common ancestor in the same region, followed by an expansion to achieve current distribution (from Mexico to eastern Brazil; Baker & Clark 1987, Gardner 2007). Other plant taxa commonly used by *U. bilobatum* that present similar distributions in the northern portion of their range are *Cryosophila* spp. This genus originated in Mexico (Evans 1995) and is currently distributed from Mexico to northern Colombia (biodiversity occurrence data accessed through GBIF Data Portal, data.gbif.org, 2010-09-06; Appendix A). The striking similarities in the current range of *U. bilobatum, Attalea* spp. and *Cryosophila* spp. (Fig. 2.6) provide working hypotheses regarding historical expansion of *U. bilobatum. Attalea rostrata* may have facilitated *U. bilobatum* expansion at least to Central America. In Panama and Costa Rica, *U. bilobatum* appears to have developed the ability to exploit *Cryosophila* spp. for tent construction, possibly

allowing further expansion of this bat species to the rest of Central America and south of Mexico.

Cryosophila spp. and *Attalea* spp. *U. bilobatum*

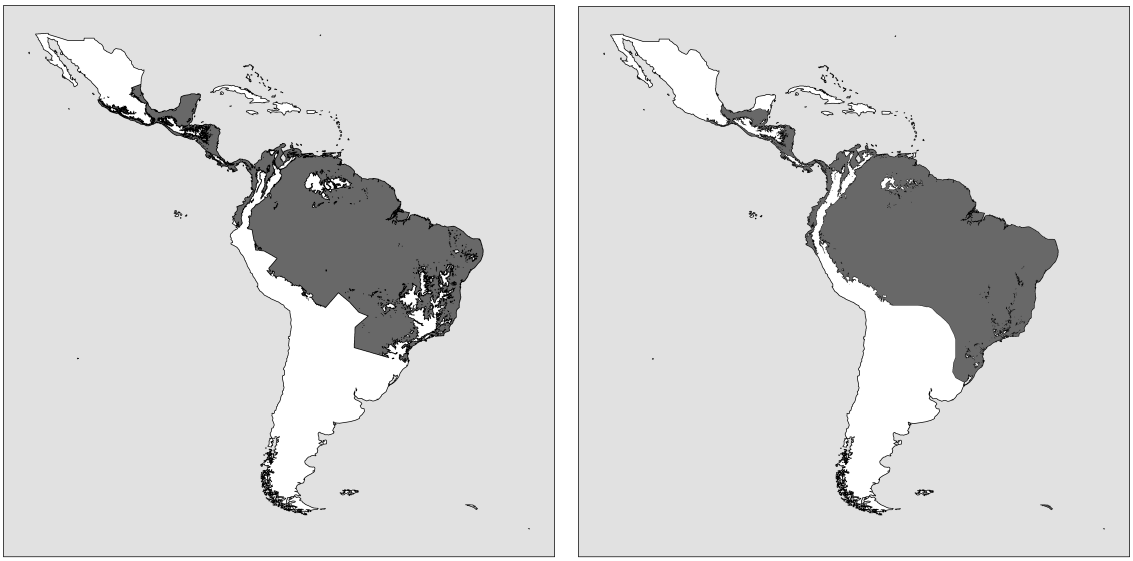

FIGURE 2.6. Current distribution of *Cryosophila* spp., *Attalea* spp. and *Uroderma bilobatum.*

At a local scale, my results suggest that current distribution of *U. bilobatum* may be influenced by abundance of plants suitable for tent construction. Moreover, introduction of non-native plants such as *C. nucifera* appear to have facilitated expansion to areas where native plants are not present, filling gaps in local distribution. This palm is native to coastal areas (littoral zone) of Southeast Asia (Malaysia, Indonesia, Philippines) (Chan & Elevitch 2006, Baudouin & Lebrun 2009) and was probably introduced into West Africa and the Caribbean (including the Atlantic and Pacific coasts of Central America) by European explorers (Harries 1978) or Polynesians (Baudouin & Lebrun 2009). Another recently introduced plant that now is widely used in human-modified areas by *U. bilobatum* is banana (*M. acuminata*). This plant was also introduced from the Indo-Malaysian, Asian and Australian tropics (Langdon 1993, Nelson *et al.* 2006). In addition, *Carludovica* spp. are used for tent construction both in forested but mainly

human-modified areas. It is native to South and Central America (Harling 1958) but has recently been used as both an ornamental and a crop plant (Harling 1958), thereby increasing its abundance in human-modified areas. Due to the rather recent introduction of these plants to Costa Rica, it is reasonable to assume that *U. bilobatum* historically roosted in native plants such as *Attalea* spp. and *Cryosophila* spp. Because the non-native plants have the preferred architecture for tent construction, upon their arrival to the Neotropics, *U. bilobatu*m has recently switched to use these plants (*i.e.* coconut palms).

IMPLICATIONS FOR CONSERVATION.— Although *U. bilobatum* is a widely distributed species, to my knowledge, this is the first study that presents a detailed description of habitat preference at different spatial scales and how this may have affected distribution and density of this Neotropical bat. I found that *U. bilobatum* is selecting habitat primarily based on microhabitat (roost characteristics), in particular, presence of plants such as coconut palms (*C. nucifera*). Distribution of *U. bilobatum* may have been positively affected by geographic expansion of plants used for tent construction.

In the last decade, there has been an increased interest on species that inhabit human-modified areas (Chace & Walsh 2006). Although it is widely accepted that knowledge of urban species will contribute significantly to preserve future global biodiversity, the ecology and distribution of urban species remain poorly understood. While *U. bilobatum* is still present in forest patches, using native plants species as roosts, I have found that it has become abundant in human-modified areas such as yards, agricultural plantations or cattle ranches. Although speculative, greater use of coconut palms in human-modified areas might be related to higher abundances of these plants, compared to native plants in forests. Differences in abundance of populations inhabiting these two different habitats can

have direct consequences on effective population size (N_e), population growth rate and consequently, on the resilience of a population to exploitation and speed of population recovery (Caro 1998). This is because higher densities alter variation in reproductive success (Caro 1998). Understanding how different environmental characteristics affect distribution and density of these populations is extremely important to define optimal management strategies able to assure long-term survival.

U. bilobatum has become a keystone species in forest fragments as it has been demonstrated that tent-roosting bats can be the last dispersers of medium-sized and large seeds in small forest patches (Melo *et al.* 2009). However, direct interaction of Peter's tent-roosting bats with humans may have negative effects at the population level. This is because lack of information and education about bats has caused people to believe that they are harmful. Consequently, communities living in areas close to forests where bats are more abundant are trying to eradicate those that roost near homes. Hence, in order to protect this important Neotropical bat, I propose strong prioritization in conservation strategies, especially through education in areas close to forest patches where this species is particularly abundant. *U. bilobatum* represents an ideal case in which to start integrating human habitats and biodiversity.

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CHAPTER 3. HABITAT EFFECTS ON GROUP GENETIC STRUCTURE AND COHESION IN PETER'S TENT-ROOSTING BATS: HOUSES MATTER

INTRODUCTION

Social organization is one of the most important features of animal societies that responds to not only ecological but also social selective pressures (Ross & Keller 1995). Since group formation has important fitness implications (*i.e.* protection from predators or enhancing thermoregulation ability, among others) understanding the mechanistic basis to group living has interested scientists for more than a century (Galton 1871). Multiple studies have suggested that animal associations and cohesiveness are enhanced by: (A) limited and patchily distributed resources (*e.g.* Altmann 1974), (B) female recruitment into natal groups followed by long-term philopatry (Castella *et al.* 2001, Kerth *et al.* 2000, Wilkinson 1985), or (C) high degrees of relatedness within groups (Ross 2001). Nonetheless, high cohesion and stability have been found in places where resources are plentiful (Rossiter *et al.* 2002) and high stability has also been reported in groups with female and/or male natal dispersal (reviewed in Clutton-Brock 1989). Moreover, individuals frequently exhibit low relatedness within colonies, even with kin selected cooperation (*e.g.* Wilkinson 1985, Wilkinson 1992, Burland *et al.* 2001, Storz *et al.* 2001a,b). Consequently close genetic ties and resource limitation alone cannot explain the variety and frequency of group stability found in nature. In contrast, ecological processes as well as variable environmental factors such as fragmentation and distribution of suitable habitats (Christiansen & Reyer 2011, Zachos & Hartl 2011) have also been indicated to be important determinants of social structure as they alter costs and benefits of sharing a territory (Bronikowski & Altmann 1996, Pusey & Packer 1997). Thus, variation in social structure should be expected among and within populations as a consequence of differences in adaptive adjustment of males and females

to differences in the ecological environment (Rubenstein 1980, Dunbar 1981, Campbell 2010, Chaverri & Kunz 2010). Although ecological factors and individual differences reflecting plasticity to adapt to different conditions are known to influence social interactions, how these factors interrelate and shape social structure has escaped the focus of contemporary research.

The rapid rate and extent of habitat modification by humans has imposed dramatic effects on natural populations, including range expansion, genetic subdivision or hybridization and extinction, among others (Dodd & Kashani 2003, Bloor *et al.* 2008, Mayer *et al*. 2009). In the last decade, there has been an increased interest in ecology and conservation of species that inhabit these human modified areas (Chace & Walsh 2006). Despite this, social structure and ecology of urban species remain poorly understood (Shochat *et al.* 2006). Here, I combine information on roosting associations with genetic structure of Peter's tent roosting bat (*Uroderma bilobatum*), to examine patterns of relatedness and group cohesion at multiple levels in forests and human-modified habitats. Peter's tent roosting bat is a medium sized (c. 17 g) phyllostomid bat that ranges from Mexico (Oaxaca and Veracruz), south to Perú, Bolivia and southeastern Brazil (Davis 1968). It is usually found below 1200 m above sea level, in a wide variety of forested and human-modified habitats (LaVal & Rodríguez-Herrera 2002). *U. bilobatum* roosts under large modified leaf structures (*i.e.* tents) of various species of plant. Tents are constructed by cutting veins and leaflets to form a semi-enclosed space (Kunz & Lumsden 2003). *U. bilobatum* forms highly gregarious groups of up to 59 individuals, which consist mostly of females and their dependent young (Baker & Clark 1987, LaVal & Rodríguez-Herrera 2002). This fruit-eating bat is a keystone in tropical forests, as it promotes plant community diversity and secondary succession (Fleming & Heithaus 1981, Fleming 1988, Gorchov *et al*. 1993). Observations indicate that *U. bilobatum* is becoming more abundant in human-altered

habitats, and may prefer to roost in introduced plant species (Tim & Lewis 1991, Lewis 1992, Sagot *et al.* submitted). If humans are facilitating use of non-natural habitats, it is critical to understand the consequences of this process on the population structure of this Neotropical bat.

When studying social systems, it is important to consider genetic structure above the level of the social group for various reasons. To begin, mating and dispersal behaviors can shape local genetic structure. Therefore, knowledge of higher-level structure can enrich understanding of determinants of colony-level structure (Wade 1994, Ross & Keller 1995, Sugg *et al.* 1996, Pamilo *et al.* 1997, Balloux *et al.* 1998). Similarly, correct evaluation of the breeding system requires knowledge of local genetic structure (Ross & Carpenter 1991, Queller *et al*. 1992, Crozier & Pamilo 1996, Chapuisat *et al.* 1997). Moreover, genetic structure of natural populations depends on both historical (*e.g.* bottlenecks, range expansion, colonization process, isolation in geographical refugia) and current factors related to species-specific characteristics such as breeding structure or gene flow (Castella *et al.* 2001). Because these processes may differentially affect the variability of biparentally and uniparentally inherited genes (Chesser & Baker 1996), independent estimates of population structure for males and females as well as use of nuclear and mitochondrial markers, provide useful information about ecological and microevolutionary characteristics of natural populations (Slatkin 1994). Therefore, my objective was to describe genetic structure, degrees of inbreeding and patterns of natal dispersal in Peter's tent-roosting bat at three different scales (group level, locality and among regions) using microsatellite markers and mtDNA. Moreover, to determine relative contributions and influence of different habitat factors on group cohesion and stability I associated group genetic structure to different habitat variables at 3 different levels: roosts (variables describing roosts characteristics), structural (habitat characteristics within habitat patches) and macrohabitat (*e.g.* land use

categories, geographical variables). Furthermore, I attempted to understand factors that can generate observed patterns such as cohesion of adult females or offspring relatedness within social groups). My results will contribute to understanding of ecological and microevolutionary processes that generate genetic structure across natural and human-modified landscapes.

MATERIALS AND METHODS

STUDY SITE AND SAMPLING.— Fieldwork was conducted at Carara National Park and surrounding areas (9°44'55.78" N, 84°37'1.29" W) in the Central Pacific versant and in the region of Sarapiquí (10°23'55.88" N, 84°08'06.23" W) in the Caribbean versant of Costa Rica between June 2007 and May 2009. These regions were selected because of differences in climate and vegetation as well as anthropogenic influence (see Sanford *et al.* 1984 and Boza & Cevo 1998 for a more detailed description). The Central Volcanic Cordillera separates both areas and is an important biogeographic barrier to dispersal in Costa Rica (Janzen 1983).

To find *U. bilobatum* in Sarapiquí and Carara, I visited all plant species known to be used as roosts (Kunz & Lumsden 2003, Rodríguez-Herrera *et al.* 2007) in forested and human-modified habitats, covering approximately the same area in both types of habitat (area determined on a georeferenced map in ArcGIS 9.3.2; ESRI 2009). In forest, I followed available trails and randomly located 10 2-km transects per site. Spatial locations of random transects were selected from a georeferenced map of the area in ArcGIS 9.3.1 (ESRI 2009). Human-modified areas were defined as plantations, grassland or urban sites. In these areas I followed available streets and roads, covering approximately the same distance covered in the forest (based on a georeferenced map in ArcGIS 9.3.2; ESRI 2009). For every plant visited, I recorded its geographic location using a Garmin GPSMAP 60CSx GPS. If bats were present, I captured the

entire group using a hand net with an extendible pole. A total of twelve social groups were used for the study. At these occupied tents, I measured habitat variables based on macrohabitat, structural and roost characteristics. Macrohabitat was defined as discrete habitats in the landscape based on land use (human-modified/ forest), site (Carara vs Sarapiquí) and distance to the forest (measured from a georeferenced map of the areas in ArcGIS 9.3.1; ESRI 2009). Structural characteristics were defined as particular habitat attributes within a macrohabitat. Structural characteristics were measured in a 20 m diameter plot around the plant being measured. Variables measured were: amount of herbaceous cover, number of bushes (woody plants with a DBH less than 20 cm), number of trees (woody plants with a DBH larger than 20 cm), average tree diameter at breast height (DBH) and average light penetration measured with a quantum light meter (Hydrofarm West, model 2053) taken at cardinal points. Finally, roost variables reflected attributes of the roosts used by bats: tent height, plant height, and plant species (*Attalea* and *C. nucifera*; each represented by a dummy variable in analyses; Suits 1957).

LABORATORY WORK.— DNA extraction: I extracted DNA from 187 *U. bilobatum* (98 adult females, 13 adult males and 76 offspring). Extractions were from liver, kidney or wing punch tissue that was preserved in lysis buffer. Extraction methods were either the PCI/phenol protocol (Longmire *et al*. 1997) or by using a Qiagen DNeasy Blood & Tissue Kit (Qiagen Inc. Chatsworth, California).

Mitochondrial DNA Sequencing: The entire cytochrome-*b* gene (1140 bases) was amplified using polymerase chain reaction (PCR; Saiki *et al.* 1988) with primers LGL765 and LGL766. The thermal profile used for amplification consisted of 94 °C for 3.5 min, 34 cycles at 94 °C for 30 s, 57 °C for 30 s, 72 °C for 1.25 min, and a final extension at 72 °C for 3 min. PCR products

were purified using QIAquick PCR Purification Kit (Qiagen Inc., Chatsworth, California) following manufacturer's instructions. DNA sequencing was accomplished using an ABI PRISM 3100-Avant (Applied Biosystems), using a set of internal sequencing primers: Uro_cytb_seq_F (5'-CGG CTT CTC CGT AGA CAA AG-3') and Uro_cytb_seq_R (5'-TGG GAT ACC TGT TGG GTT GT-3') designed for this study. The thermal profile used for sequencing consisted of 94 °C for 4 min, 34 cycles at 94 °C for 30 s, 57 °C for 30 s, 60 °C for 4 min. Sequences were verified and aligned using Sequencher version 4.9 (Gene Code Corporation, Ann Arbor, Michigan).

Microsatellite genotyping: To develop a microsatellite library for *U. bilobatum,* I sent approximately 70 µg of total genomic DNA to Duke University's Genome Sequencing and Analysis Core Facility 454 Titanium Sequencing Services. This library was barcoded and run on the equivalent of 1/8 plate. The file containing raw sequence data from the 454 shotgun sequencing was analyzed using Primer Designer (Castoe *et al.* 2010). This is a Perl script that extracts reads that are at least 12 base pairs (bp) in length and inputs those reads into Primer3 (Rozen & Skaletsky 2000). Primer3 criteria for primer design were: 58–65 °C melting temperature (Tm) with <2% difference between paired primers and optimal Tm of 62 °C, GC content 30–80%, a GC clamp on the last 3 nucleotides, amplicon length of >60 bp, max poly-N of four nucleotides and primer size 18–30 bp with optimal size of 20 bp. Other parameters were set to Primer3 default values.

The resulting output file returned 13,805 reads with microsatellites. The criteria used to select primers for analyses were: tri or tetra-nucleotide repeats, >6 tandem repeats and unique occurrence of the forward and reverse primer in all reads. Of 220 microsatellite primers (forward and reverse) that met those criteria, I randomly selected 120 primer pairs to test for amplification

of genomic DNA used for 454 sequencing. From primers that amplified, I selected loci that produced a single strong band of PCR product. These loci were used to test for polymorphism by genotyping eight *U. bilobatum* samples (two from Costa Rica, three from Ecuador and three from El Salvador). I used the following thermocycler settings: 94 °C for 3.5 min, 34 cycles at 94 °C for 30 s, 54, 57 or 60 °C (depending on the annealing temperature of the primers) for 30 s, 72 °C for 1.25 min, and a final extension at 72 °C for 5 min. All PCR's were performed in a final volume of 50 µL with the following reagents: 1 µL of 25 – 80 ng/lL DNA template, 1 µL of Taq DNA polymerase, 5 µL of 2 pmol forward and reverse primer each, 5 µL of 10X buffer, 5 µL of 8 mm dNTP, and molecular biology grade H_2O to reach final volume. Amplification and polymorphism was first assessed by running 5 µL of PCR product on a 5% agarose gel. After these tests, a subset of 13 loci were selected for genotyping. Three of these loci were not in Hardy-Weinberg equilibrium and were eliminated from analyses (Table B.1).

Before genotyping, new sets of forward primers with a M13 (-21) tail at its 5' (Schuelke 2000) were obtained. I used a step-down thermocycler profile as proposed by McCullogh & Stevens (2011). Specific thermocycler settings were as follows: 94 °C for 5 min, then 10 cycles at 94 °C for 30 s, 60 °C for 45 s, 72 °C for 60 s, bumping down 1 °C every cycle, followed by 25 cycles at 94 °C for 30 s, 50 °C for 45 s, 72 °C for 60 s, and a final extension at 72 °C for 10 min. Additionally, I added a universal fluorescently-labeled M13(-21) (either FAM or HEX). Schuelke (2000) suggests that the reverse and M13 fluorescently labeled primers should be used in equal concentrations, while the forward primer should be a fourth of the concentration of the other two primers. Therefore, 1 µL of 2 pmol forward and 1 µL each of 8 pmol reverse primer and 8 pmol M13 fluorescently labeled universal primers were used for all reactions. Samples were genotyped on an ABI PRISM 3100-Avant (Applied Biosystems). Genotypes were

determined in GeneMapper version 4.0 (Applied Biosystems).

ANALYTICAL APPROACH.— Spatial genetic structure: Collapse v1.2 (available from http://darwin.uvigo.es), a software that collapses cyt*b* sequences into haplotypes, was used to determine the number and frequency of unique haplotypes among sampled social groups. A cyt*b* haplotype network was constructed on TCS v1.21 (available from http://darwin.uvigo.es) using the unique haplotypes found. This program is a cladogram estimation method that determines gene genealogies (*i.e.* genealogical relationship of genes at a locus) from DNA sequences as described by Templeton *et al.* (1992) and maps unique haplotypes onto this cladogram (Clement *et al.* 2000). Distributions of haplotypes among social groups were mapped onto this network.

To determine if groups and populations are genetically structured and differentiated, I calculated pairwise F_{ST} values for microsatellite data using the software ARLEQUIN v3.1 (Excoffier *et al.* 2005). I did this at the group scale (pairwise F_{ST} among the twelve social groups), locality (pairwise F_{TS} comparing different localities within Sarapiquí and Carara) and regional (pairwise F_{ST} comparing Sarapiquí and Carara) scale. Values were tested for significant differences within levels using 10,000 permutations (sequential Bonferroni method implemented in ARLEQUIN). Moreover, to determine if patterns of population differentiation are associated with geographic distance between social groups, I performed an isolation-by-distance analysis using the IBD Web Service v3.21 (IBDW 3.21; Jensen *et al.* 2005). This program performs a Mantel test between a geographic and genetic distance matrix and estimates a R^2 and its statistical significance by permuting data 30,000 times. The genetic distance matrix was calculated in ARLEQUIN v3.1 (Excoffier *et al.* 2005) and the geographic distance matrix was calculated from geographic coordinates using ArcGIS 9.3; ESRI 2009). Both matrices were log-

transformed prior to analysis as suggested by Slatkin (1993) and Hutchison & Templeton (1999).

To evaluate spatial genetic structuring, I used an individual-based approach as implemented in the program STRUCTURE (Pritchard *et al.* 2000). This is a Bayesian model-based clustering method that assigns individuals to populations based on multilocus genotypes (Pritchard *et al*. 2000). For K population clusters, this program estimates the probability of the data and individual membership in each cluster using a Markov chain Monte Carlo method (MCMC). The program was run assuming correlated allele frequencies and admixture as suggested by Pritchard *et al.* (2000). I conducted three independent runs for each value of K, to estimate the true number of clusters. I used 100,000 iterations after a burn-in period of 1,000,000 iterations. The number of populations best fitting the data was determined using the log probability Pr(X|K) and ΔK, as described by Evanno *et al.* (2005) and implemented in the program STRUCTURE HARVESTER (Dent *et al.* 2011). A total of 12 social groups were used for the analysis. The simulated value of K ranged from 1 to 12. Moreover, I combined social groups by locality within regions to determine if localities where structured. Because I had a total of 7 localities (4 in Carara and 3 in Sarapiquí), simulated K ranged from 1 to 7. I also combined localities within regions to determine if populations were structured at a regional scale (Carara and Sarapiquí). In this case K ranged from 1 to 2. Moreover, I ran STRUCTURE separately for adult males, adult females and offspring to explore if the K found when combining all sexes and ages was influenced by the structure of adult females, adult males or offspring within social groups. The simulated K value in this case ranged from 1 to 12.

To determine if more stable social groups show high levels of inbreeding, I performed a single regression to compare adult female and offspring inbreeding coefficients among 12 social groups (F_{IS}; calculated in ARLEQUIN v3.1; Excoffier *et al.* 2005). This test was performed in R

v2.10 (R Development Core Team 2009).

Habitat effects on group cohesion: To determine relative contribution of roost, structural and macrohabitat levels to group cohesion, I performed variance partitioning analyses (Legendre & Legendre 1998) whereby group fixation index (F_{IS}; calculated in ARLEQUIN v3.1; Excoffier *et al.* 2005) was the dependent variable and the different habitat levels represented three independent explanatory matrices. This test characterizes: (1) unique variation explained by a particular level (*i.e.* macrohabitat, structural or roost) after controlling for the other two levels, (2) correlated variation explained by each two-way interaction, (3) correlated variation explained by all three individual matrices and (4) variation not accounted for by any individual matrix. Partitions are independent and additive summing to 100%. Tests were conducted in VarCan (version 1, Peres-Neto *et al.* 2006). If a level or levels contribute significantly to variation in F_{IS}, I then performed a multiple regression between F_{IS} and variables within that level to determine which particular variables were contributing more to the explained variance. These tests were performed in R v2.10 (R Development Core Team 2009).

Since groups are formed by one or two adult males, multiple adult females and their offspring, overall patterns in group structure might be driven by relatedness of the adult females and/or of offspring within social groups. If the pattern is driven by offspring, I expect offspring within social groups to be sired exclusively by harem males. Moreover, offspring should show a habitat gradient resembling the overall pattern determined by the above-mentioned variance partitioning analyses. On the other hand, if relatedness among only adult females is driving the overall pattern, I expect to find that their relatedness pattern exhibits a habitat gradient similar to the overall pattern. To determine which of the two predictions is better supported, I performed variance partitioning analyses for adult female and offspring separately based on fixation indexes

and habitat levels as explained above. Group, adult female and offspring fixation indexes were calculated in ARLEQUIN v3.1 (Excoffier *et al*. 2005).

Additionally, I performed a paternity analysis in order to determine degree of male monopolization and extra-pair/extra-group mating patterns. Paternity assignment was calculated using a maximum likelihood-based method described in Marshall *et al.* (1998) and implemented in the program CERVUS v3.0 (Kalinowski *et al*. 2007). CERVUS first calculates the frequency of each allele for each locus in the population, as well as summary statistics such as Hardy-Weinberg equilibrium and presence of null alleles. It incorporates occurrence of null alleles, mutations and incomplete sampling into likelihood calculations to decrease the probability of false exclusions. Moreover, it performs a simulation of parentage analysis to examine feasibility of the analysis given a set of loci. It also calculates values of likelihood ratios based on allele frequencies and number of candidate parents. These values are used in the parentage analysis to determine confidence of parentage assignments. Finally, CERVUS assigns to each offspring tested, the most-likely candidate parent with a pre-determined level of confidence. Input parameters used in the simulation module included: (1) number of simulated offspring based on 10000 iterations, (2) candidate parents (adult males found in study sites), (3) proportion of candidate parents sampled (estimated from field observations), (4) proportion of loci typed (calculated in the allele frequency module), and (5) the proportion of loci mistyped (calculated from known parent–offspring genotype mismatches in the allele frequency module). All males (N =13) were considered as potential fathers for each offspring. Paternity likelihood was estimated using the ratio of probabilities (LOD score). I examined whether the sampled offspring (N = 76) could be assigned to the harem male.

I was not able to sample all males in my study sites. To estimate the number of males siring offspring within social groups, I identified paternal half-siblings (offspring that share the same father) among pups roosting in the same tent. To do this, I used a likelihood-based method, implemented in the program KINSHIP v1.3 (Goodnight & Queller 1999), and allele frequencies generated in CERVUS. KINSHIP performs maximum likelihood tests of pedigree relationships between pairs of individuals. The program calculates likelihood ratios when comparing a hypothesis of relatedness for all possible individual pairs in the data set to a null hypothesis of no relatedness.

I calculated the log-likelihood ratio that shared alleles are identical by paternal descent (Rp= 0.50, Rm=0.00), and compared this to a null hypothesis in which alleles are not identical by descent through either route of Mendelian transmission (Rp = 0.00, Rm =0.00). I then performed 1000 pairs of simulation routines to generate a probability of the likelihood ratio for each pair. Offspring were identified as paternal half-siblings if the P-value for that dyad was smaller than 0.05.

RESULTS

SPATIAL GENETIC STRUCTURE.— I identified 49 unique cyt*b* haplotypes distributed among 12 social groups (Fig. 3.1) suggesting female natal dispersal and low genetic structure. The most common haplotype was present in 28 individuals distributed across 7 groups. Two other haplotypes were fairly common, occurring in 23 and 17 individuals and distributed among 6 and 5 groups respectively. The remaining haplotypes occurred at low frequencies and were sometimes found in more than one social group, but often only occurred in a single group.

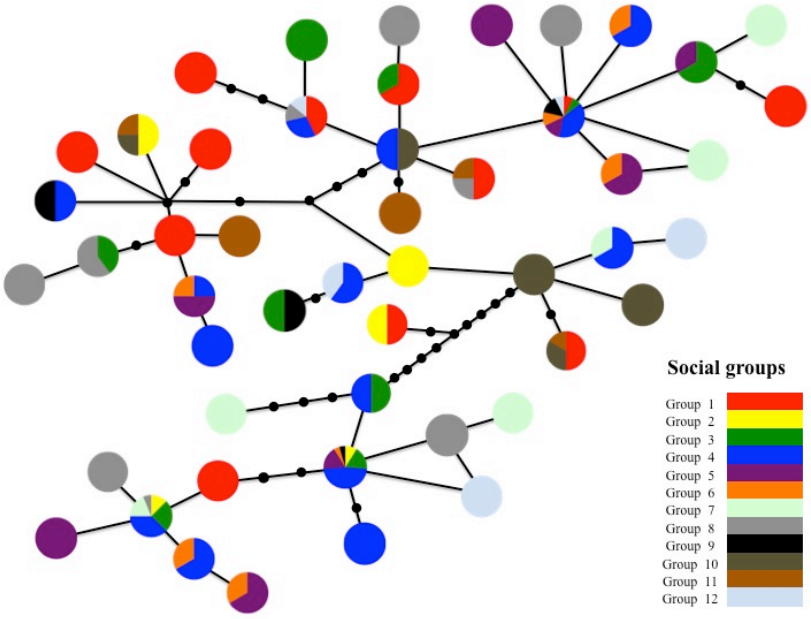

FIGURE 3.1. Haplotype network of sampled *U. bilobatum*. Colors represent different social groups. Each black line between black points indicates one point of mutation. Groups 1 2, 3, 11 and 12 are from Sarapiquí. Groups 4, 5, 6, 7, 8, 9 and 10 are from Carara.

Pairwise F_{ST} among social groups revealed that group 1 and 2 are significantly different from other social groups (Table 3.1).

TABLE 3.1. F_{ST} values and significance between 12 Peter's tent-roosting bat (*Uroderma bilobatum*) social groups in Costa Rica. Groups 1 2, 3, 11 and 12 are from Sarapiquí. Groups 4, 5, 6, 7, 8, 9 and 10 are from Carara.

Groups	1	2	3	4	5	6	7	8	9	10	11	12
1	0.000											
2	0.029	0.000										
3	0.092 *	0.147 *	0.000									
4	0.098 *	0.166 *	0.009	0.000								
5	0.120 *	0.208 *	0.035	0.013	0.000							
6	0.065 *	0.122 *	0.013	0.032	0.051 *	0.000						
7	0.106 *	0.136 *	0.013	0.049 *	0.098 *	0.013	0.000					
8	0.126 *	0.174 *	0.011	0.055 *	0.081 *	0.025	0.006	0.000				
9	0.068 *	0.103 *	0.050 *	0.065 *	0.092 *	0.005	0.053 *	0.078 *	0.000			
10	0.117 *	0.172 *	0.034	0.037	0.029	0.032	0.066	0.065	0.055	0.000		
11	0.073 *	0.128 *	0.008	0.007	0.029	0.005	0.028	0.038	0.025	0.007	0.000	
12	0.134 *	0.206 *	0.019	0.025	0.017	0.036	0.049	0.042	0.094 *	-0.005	0.028	0.000

*Pvalue < 0.005

Group 9 differed from the other groups except groups 11 and 12. The other 9 groups are relatively similar to each other (Table 3.1).

At the locality scale, within Sarapiquí social groups were significantly different from each other (Table 3.2). However, within Carara, localities were not differentiated. At a regional scale, groups from Sarapiquí and Carara were significantly different (F_{ST} = 0.074, $P \leqq 0.001$). However, after performing an AMOVA to define if variation was contained within or among regions, I was able to determine that 92.57% is comprised within region and only 7.43% among regions (*d.f* = 1, 372; $P \leqq 0.001$). Moreover, these differences are not associated with geographic distance; euclidean distance between social groups did not explain significant variation in microsatellite genetic distance (IBD, Mantel Test: R^2 = 0.143, P = 0.143).

TABLE 3.2. F_{ST} values and significance between Peter's tent-roosting bats (*Uroderma bilobatum*) from four different areas in Sarapiquí, Costa Rica.

Areas	Virgen	Centro	Tirimbina	Finca
Virgen	0.000			
Centro	0.029	0.000		
Tirimbina	0.117 *	0.172 *	0.000	
Finca	0.073 *	0.128 *	0.007	0.000

*Pvalue < 0.005

Structure analyses revealed a maximum Pr(X|K) for K = 2 (Fig. 3.2A). This result was consistent at group, locality and region levels; therefore only results from group level are reported here. To investigate if adult females, adult males and/or offspring within groups influenced this pattern, I performed STRUCTURE analyses separately for these three categories. For females, structure revealed a maximum Pr(X|K) for K = 5 (Fig. 3.2B). For males I obtained a

maximum Pr(X|K) for K = 3 (Fig. 3.2C). Offspring showed a maximum Pr(X|K) for K = 2 (Fig. 3.2D). This suggests that females exhibited more structured groups than offspring and males.

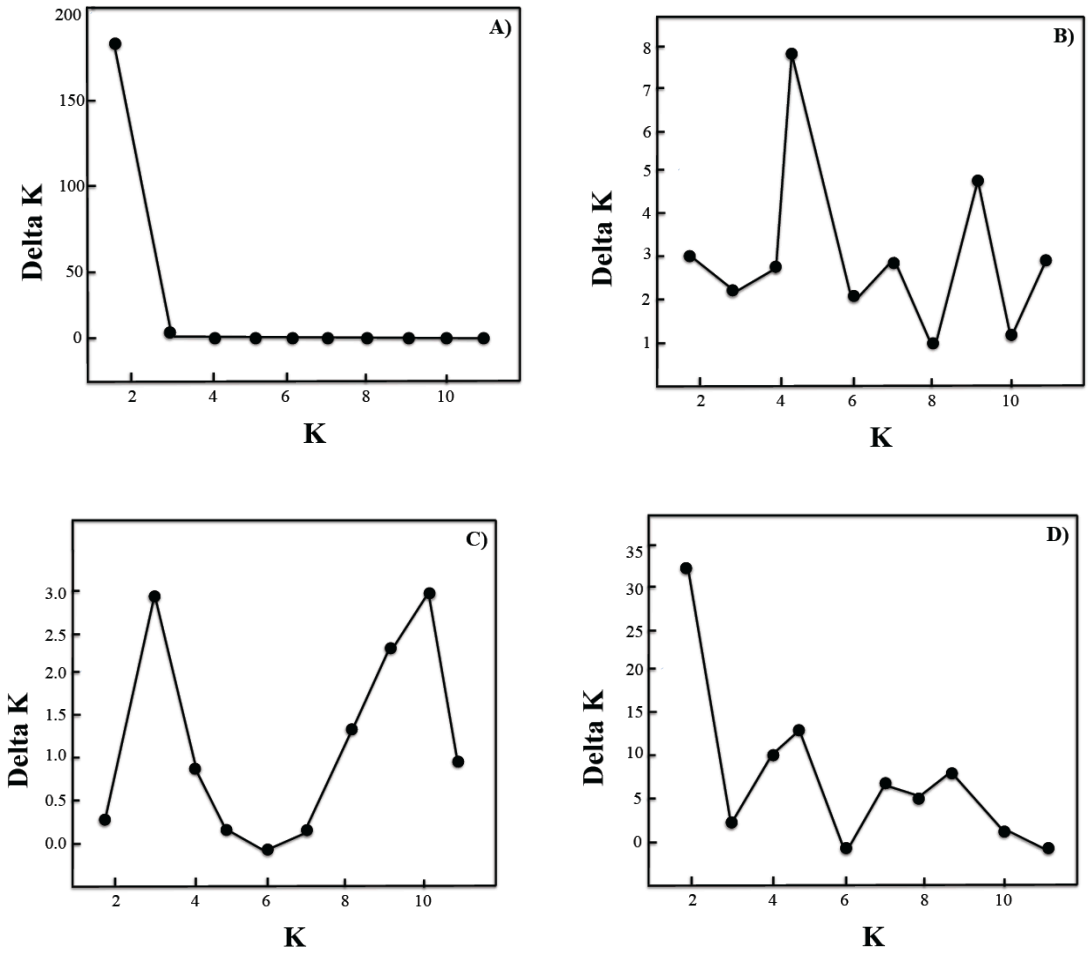

FIGURE 3.2. Change in Delta K based on Evanno (2005) for 3 STRUCTURE runs with K ranging from 1 to 12 for **(A)** all *Uroderma bilobatum* in my study sites, **(B)** only adult females, **(C)** only adult males and **(D)** only offspring. DeltaK = mean(|L"(K)|) / sd(L(K)).

There was a negative and highly significant regression between adult female and offspring F_{IS} within groups ($R^2 = 0.72$; $F_{1,8} = 21.32$; $P = 0.001$; Fig. 3.3). In social groups where adult females were more closely related to each other, offspring exhibited lower F_{IS} values.

Moreover, groups with less related adult females were associated with more related offspring (higher F_{IS}).

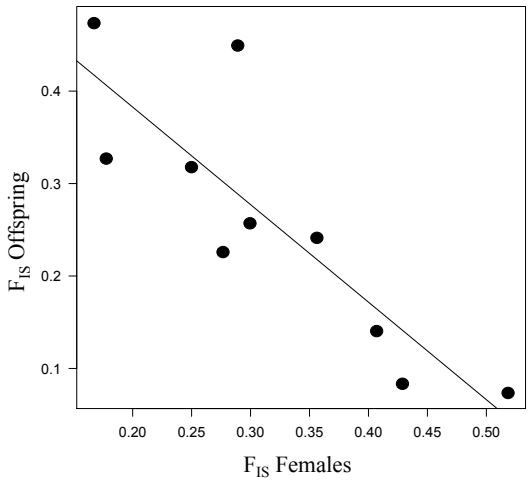

FIGURE 3.3. Regression between Peter's tent roosting bat adult female and offspring fixation indexes (F_{IS}) within social groups in Costa Rica.

HABITAT EFFECTS ON GROUP STRUCTURE.— All three habitat levels (macrohabitat, structural and roost) combined explained 80% of the variation in the fixation index (F_{IS}) for all individuals within social groups ($P = 0.001$; Fig. 3.4A). From this explained variation, roost characteristics had the highest predictive power (40%) and it was the only level that accounted for significant variation. Multiple regression between F_{IS} and variables from the roost level demonstrated that more cohesive groups (*i.e* higher F_{IS}) are found in coconut palms (*Cocos nucifera*) with heights that ranged from 7 to 10 m or tents with heights that ranged from 10 to 15 m ($R^2 = 0.4$; $F_{4,10}=3.7$; $P = 0.04$). Results suggest that groups using roosts high off the ground and in coconut palms are more cohesive.

OFFSPRING DRIVEN PATTERN.— To determine if structuring of offspring in social groups reflected habitat effects on overall group structure, I first performed a paternity analysis. Mean

number of alleles per locus found was 9.4. Additionally, mean expected heterozygosity and mean polymorphic information content were 0.61 and 0.58 respectively. On a strict level (95% confidence), fathers were assigned to only 18 out of 76 offspring (24%) and at a relaxed level (80% confidence) fathers were assigned to 39 offspring (51%).

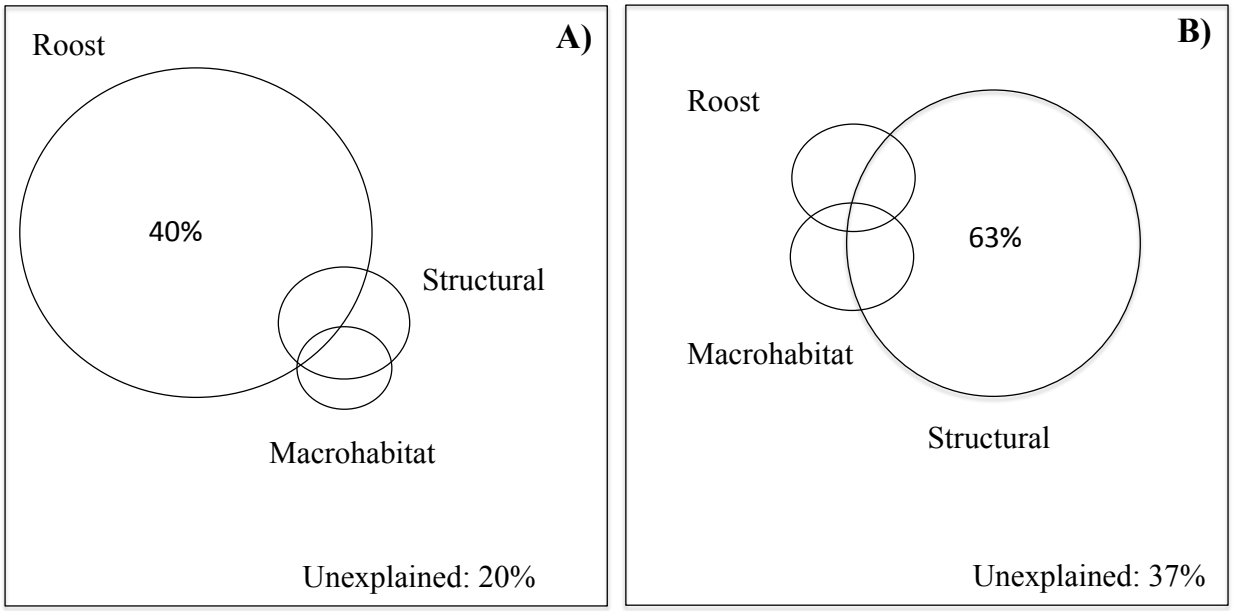

FIGURE 3.4. Variation partitioning analysis to determine roost, structural and macrohabitat effects on **(A)** overall groups F_{IS} and **(B)** adult female F_{IS}. Each box represents 100% of the variation. The summed areas of the 3 circles represent the overall variance explained. The area of any circle that is not overlapping any other represents the unique variance explained by each individual habitat perspective. The area of any two overlapping circles represents variance explained by the interaction of 2 habitat perspectives. The area where the three circles overlap represents the variance explained by the interaction of the 3 habitat levels. Non-significant variances are not reported.

Subsequently, since I was not able to capture all adult males that inhabit my study sites, I calculated the probability of sharing the same father, to estimate the number of fathers siring offspring in social groups. I found that within a social group there were on average 3 males siring offspring (Table 3.3). Variance partitioning analysis demonstrated that no significant variation in offspring F_{IS} could be attributed to any variable measured at any level ($P = 0.211$).

TABLE 3.3. Number of offspring per group and average number of males siring offspring in *U. bilobatum*. Number of fathers were determined in CERVUS and KINSHIP.

Group	Number of offspring	Number of fathers
1	11	3
2	4	1
3	9	6
4	24	7
5	10	4
6	4	4
7	3	3
8	3	3
9	5	3
10	4	3

FEMALE DRIVEN PATTERN.— To determine if the overall pattern of habitat effects of group F_{IS} was influenced by structuring of adult females within social groups, I performed a variance partitioning analysis between habitat levels and female F_{IS}. The analysis demonstrated that female F_{IS} exhibits a habitat gradient (63%, $P = 0.001$, Fig. 3.4B). The structural level mainly explained variation. This suggests that relatedness of adult females within social groups is related to habitat variation. Females showed higher F_{IS} in places with small number of trees and low light abundance ($R^2 = 0.6$; $F_{5,6} = 4.4$; $P = 0.04$).

DISCUSSION

Analyses of genetic structure and variation across multiple scales using mtDNA and nuclear microsatellite markers revealed that Peter's tent-roosting bats do not show significant broad scale geographic structure. Regions (Sarapiquí and Carara) were found to be significally different from each other ($F_{ST} = 0.074$, $P \leqq 0.001$), which was expected, as they are at least 80 km apart. However, the small F_{ST} value and results of IBD suggested that most of the genetic

variation in *U. bilobatum* is contained within social groups and localities and not at the regional level. Data revealed distinctive patterns in the genetic structure of different suites of group members (adult males, adult females or offspring). When dividing analyses by these 3 different types of group members, I was able to determine that adult females are more structured, as estimated by 5 distinct populations. This suggests that adult males and offspring, which showed more panmictic populations, drove the overall patterns of no structure.

PATTERNS IN SPATIAL GENETIC STRUCTURE.— Peter's tent-roosting bats do not have well-structured populations throughout the study area. This was demonstrated both at the mitochondrial and nuclear level. Unique haplotypes were shared among different social groups, localities and regions (Fig. 3.1). Lack of structure between social groups regarding mtDNA suggests that females are not philopatric and might disperse from their natal groups. This pattern is not common in mammals. In many mammalian species, males disperse from their natal area, while females remain philopatric (Greenwood 1980). Occurrence of female-biased dispersal has been coupled with resource-defense polygyny (Greenwood 1980). In these cases, males defend a valuable resource for females such as refuges and females distribute around these resources. Greenwood (1980) proposed that males have better chance to acquire breeding territories in natal areas than elsewhere due to familiarity with the locality. Moreover, if competition for resources is high and a proportion of males are prevented from breeding, males that are able to hold defendable resources might have more chances of mating if they stay in the same area (Greenwood 1980). In these cases, the ability of males to defend a resource may promote female dispersal in order to avoid inbreeding, if male tenure exceeds female age at first conception (Clutton-Brock 1989). Although no specific information is available for *U. bilobatum* on age at

first conception, it is known that average age of maturity for phyllostomids is 4.6 months (Barclay & Harder 2003). Furthermore, another related tent-roosting bat, *Dermanura watsoni* reaches sexual maturity at around 50 days after birth (Chaverri & Kunz 2006). Younger age at sexual maturity is advantageous in foliage roosting animals because the vulnerable roosting conditions favor pups that attain flight and foraging independence faster (Chaverri & Kunz 2006). Thus, since *U. bilobatum* is a foliage roosting bat, we might expect a similar developmental rate. Moreover, since males have been found using the same tent or plant in multiple years (M. Sagot not publ; data based on mark-recapture), in *U. bilobatum*, male tenure appears to exceed age at first conception. Likewise, negative correlation between female and offspring $F_{IS,}$ coupled with female natal dispersal suggests mechanisms for inbreeding avoidance in Peter's tent-roosting bats possibly related to male extended tenure.

OPTIMAL INBREEDING.— Extent of inbreeding avoidance depends on its relative cost, compared to outbreeding (Waser *et al*. 1986, Kokko & Ots 2006, Olson *et al*. 2012). High costs of avoidance, such as delayed reproduction if unrelated males are not available, or decreased survival due to diseases, leads to inbreeding tolerance in natural populations (Pusey & Wolf 1996, Olson *et al*. 2012). In *U. bilobatum*, the negative correlation between female and offspring F_{IS}, as well as the paternity patterns found (multiple males siring pups within groups), suggest that when females within groups are more related to each other, they engaged in extra-pair/extra-group mating with males, possibly to avoid mating with the same harem male at multiple reproductive seasons. In this species, it is common to find other social groups and/or solitary males in neighboring tents or palms (Timm & Lewis 1991, Lewis 1992). Therefore, finding unrelated males is not time consuming or energetically costly for *U. bilobatum* females.

Moreover, in the majority of studies, inbreeding has been associated with lowered offspring birth weight (Coltman *et al.* 1998). This is problematic for bats, because it increases nutritional dependency on mothers and makes it harder to thermoregulate (Kurta & Kunz 1987). Extended periods of maternal care enhance exposure of females to nocturnal predators, due to more extensive time spent travelling back and forth to the roost. Moreover, inbreeding has also been coupled with decreased parasite resistance (Acevedo-Whitehouse *et al*. 2003). Infectious diseases have been implicated in die-offs of large maternal colonies (*i.e.* white nose syndrome and herpes virus [Roue & Nemoz 2004, Blehert *et al.* 2009]). Since *U. bilobatum* appears not to be affected by high costs of inbreeding avoidance and might benefit from reduced fidelity by obtaining good genes and finding high quality males (Jennions & Petrie 2000, Di Battista *et al*. 2008), it is not surprising to find inbreeding avoidance mechanisms in this species. Although no detailed studies on inbreeding are available for other foliage roosting species, similarities in their ecological requirements and behavior suggest that inbreeding avoidance mechanisms might be widespread among these bats.

Excessive outbreeding is also detrimental in natural populations as it causes disruption of locally adapted gene complexes that are beneficial to adapt to immediate environments (Lynch 1991). Thus, prevention of excessive outbreeding also benefits populations. Multiple studies have proposed a level of optimal inbreeding, in which individuals avoid extreme outbreeding and close inbreeding by mating with partners of intermediate relatedness (Bateson 1982, 1983, Hoogland 1992, Peacock & Smith 1997). This may to be the case in *U. bilobatum.* I have found that in groups in which females have low F_{IS}, offspring have higher F_{IS}. Optimal inbreeding levels based on mate choice have also been reported in other vertebrates. For example female Japanese quail, *Coturnix coturnix* (Bateson 1980, 1983) and white-footed mice, *Peromyscus*

leucopus (Keane 1990) preferred to mate with males of intermediate relatedness, instead of siblings or non-relatives. Moreover, female house mice, *Mus musculus* preferred slightly unfamiliar males, rather than close relatives or unknown males (D'Uline & Alleva 1985). Two mechanisms were proposed by Bateson (1983) to explain choice of mates of intermediate relatedness: (A) short distance dispersal; and (B) kin recognition. Spatial genetic structure and unique haplotypes' distribution in *U. bilobatum* suggest that females are dispersing long distances, although some groups might become more cohesive and possibly philopatric when roosting in specific roosts. In contrast, to give rise to the pattern obtained (negative correlation between offspring and female F_{IS}), females should be able to recognize male relatedness. This is because females that live in cohesive groups appear to mate with less related males, and less related group of females seem to be mating with more related males. Multiple studies in different vertebrates have determined that some species can discriminate mates via olfaction (*e.g*. Meaney 1983, Olsén *et al.* 1998, 2002, Novotny *et al.* 2007). Moreover, various studies on the major histocompatibility complex genes (MHC) in multiple vertebrate species propose that preferences for mates carrying dissimilar MHC genes may help animals avoid inbreeding (Brown 1997, Jennions & Petrie 2000, Tregenza & Wedell 2000, Neff & Pitcher 2005, Bonneaud *et al.* 2006, Huchard *et al*. 2010). Recognition of kin or related/unrelated individuals via MHC genes is mediated by MHC-dependent odors, which are recognized by chemoreceptors (Ziegler *et al*. 2005). Ligand–receptor interactions lead to neuronal responses that ultimately influence social and mating behaviors such as female choice (Ziegler *et al*. 2005). However, more detailed studies on the social behavior of Peter's tent-roosting bats and the genetic basis for such behaviors are needed to further elucidate these results.

HABITAT EFFECT ON GENETIC STRUCTURE.— Formation of cohesive groups has been reported in many bat species (*e.g.* Wilkinson 1985, Heckel *et al.* 1999, Kerth *et al*. 2000, Vonghof *et al*. 2004). Most plausible hypotheses to explain these cohesive associations include knowledge of suitable foraging and roosting sites, thermoregulation, avoidance and reduced exposure to parasites and diseases, cooperation, etc, (Allen 1962, Emlen 1994, Clutton-Brock 2002, Kerth *et al*. 2002, Altizer *et al.* 2003, Calisher *et al.* 2006, Kerth 2008). Moreover, because it is widely known that variation in genetic relatedness could be a consequence of adaptation to different habitat conditions (Rubenstein 1980, Dunbar 1981, Chaverri & Kunz 2010), I tested if different habitat variables at different levels were able to explain some of the patterns found in the genetic structure of *U. bilobatum*. I found that roost characteristics were able to explain most of the variation in the fixation index (F_{IS}) of Peter's tent-roosting bat groups. This indicates that groups roosting in plants with specific characteristics (*e.g.* made in coconut palms with heights ranging from 7 to 10 m) exhibit more stable and structured social groups. Roosts are valuable resources for bats because they provide a space to carry out social interactions, they may be relatively scarce (Kunz 1982, Kunz & Lumsden 2003) and costly to construct (Balasingh *et al.* 1995, Kalko *et al*. 2006, Rodríguez-Herrera *et al.* 2007). Thus, it should not be surprising that roosts are one of the most important determinants of social systems in many bat species (Chaverri & Kunz 2010). However, to date, significance of roosts in social interactions has been overlooked and poorly understood (but see Sagot & Stevens 2012).

Since groups are formed by 1 adult male, multiple adult females and their offspring, I investigated if the overall pattern in group structure was driven by average relatedness of females, offspring or both. I determined that multiple males sire offspring within social groups, suggesting that offspring are moderately outbred. Multiple paternity is common in many taxa

(Møller & Birkhead 1993, Griffith *et al*. 2002, Isvaran & Clutton-Brock 2007). Males benefit from mating with multiple females because they enhance their reproductive fitness. In females, such behavior is less likely to enhance their fitness due to high costs associated to parental care and disease transmission, among others (Bateman 1948, Trivers 1972, Daly 1978, Magnhagen 1991, Lombardo 1998, Wolff & Macdonald 2004). Nonetheless, costs associated to multiple mating in females can be reduced if it increases offspring fitness such as inbreeding avoidance, compared to single mating (Jennions & Petri 2000, Birkhead & Pizzari 2002, Wolff & Macdonald 2004). Based on the inbreeding patterns found in this study, this may be the case in Peter's tent-roosting bats.

Extra-group paternity (males other than harem male siring offspring) is especially likely in Peter's tent-roosting bats due to the nature of their roosting ecology. Roosts built in coconut palms (*C. nucifera*) are the most frequently used by *U. bilobatum* (Sagot *et al*. submitted) and are the roost type where groups show higher relatedness. Coconut palm roosts are highly clumped and remain usable across multiple mating seasons (Sagot *et al.* submitted, Sagot & Stevens 2012). Moreover, male roost fidelity is high for these palms and maximum harem sizes are larger than those reported from roosts constructed from other plant species (Sagot *et al.* submitted). Since clumped distribution of desirable roosts promotes clumped distribution of males, females can potentially sample and mate with any of a number of males in the surrounding area. (Campbell *et al.* 2006, Gopukumar *et al*. 2005, Storz *et al.* 2000A,B). This behavior has been reported for various bat species of the genus *Cynopterus* (Campbell 2010).

I also predicted that if offspring relatedness explains the habitat gradient found for group F_{IS}, offspring F_{IS} should also exhibit a habitat gradient. Nevertheless, I found that habitat variables did not have a significant effect on offspring F_{IS}. The relationship between habitat

variables and female F_{IS} suggests that female genetic structure may be driving the observed pattern. Although the structural instead of the roost level drove the pattern for female F_{IS}, the variables that were found significant (*i.e*. small number of trees), were characteristic of habitats where coconut palms were found (*i.e*. open areas). This is because other plant species used for tent construction are only present in forests, where the number of trees surrounding tents is high. This suggests that females prefer open habitats where coconut palms are abundant. Moreover, high levels of group relatedness in specific coconut palms suggest that during nursing periods adult females prefer palms and tents with specific heights. Variation in female relatedness among groups has also been reported in other bats species (*A. jamaice*nsis [Kunz & McCracken 1996, Morrison 1979, Ortega & Arita 1999], *D. watsoni* [Chaverri *et al.* 2007], *Neoromicia nanus* [Happold & Happold 1996, O'Shea 1980], and *Cynopterus sphin*x [Storz 2001B]). The fact that we can detect some structure in adult females at the microsatellite level, but not at the mitochondrial level, may be a reflection of the ephemeral duration of roosts (up to 2 years) and habitat conditions around them. Adult females and daughters are able to use the same roost or plant for some years (Lewis 1992), but when conditions become unsuitable for them, they might move to establish their residence at a different site. There is no information on how long a particular palm can be suitable for bats, but observations suggest that some palms can be used for more than 20 years (palms first reported as roosts by Timm and Lewis (1991) in 1988, were still occupied in 2007. M. Sagot. pers. obs.). Based on *U. bilobatum* generation time and reproductive patterns (two reproductive seasons per year, with one offspring per season; Baker & Clark 1987), this period of time might be enough to detect some structuring at the microsatellite level (10^{-3} or 10^{-4} base pairs per locus, per gamete per generation; Weber & Wong 1993, Primmer *et al.* 1996, Schug *et al.* 1997, Lai & Sun 2003), but not long enough to fix

mitochondrial haplotypes within social groups. Moreover, the fact that these groups are formed by multiple maternal lines suggests that roosting associations occur between unrelated, as well as related females. This indicates that relatedness is not essential for social relationships to be established. This pattern has also been found in the Benchstein's bat, *Myotis bechsteinii* (Kerth *et al.* 2011, Kerth *et al*. 2012).

When examining tent density, it is common to observe plants with multiple tents while other plants posses only one or none (Timm & Lewis 1991, Sagot *et al.* submitted). Plants with more than one tent are usually occupied more often, suggesting that bats prefer particular roosting sites over others (Timm & Lewis 1991, Sagot *et al*. submitted). The fact that these preferable roosts are common at both regions (Carara and Sarapiquí; Sagot *et al*. submitted), might help to explain the lack of geographic structure and influence of macrohabitat variables on group cohesion in Peter's tent-roosting bats.

CONCLUSIONS.— My findings suggest that although *U. bilobatum* has low spatial genetic structure, female group composition can sometimes be stable owing to a tendency of females to aggregate. These patterns were evident in tents constructed from coconut palms (*C. nucifera*) with heights ranging from 10-15 m and tents with heights ranging from 8-10 m. My study suggests that variation in these natural structures is related to variation in the degree of group cohesion and stability within *U. bilobatum*. Tent roost use appears to have favored a harem-based social structure. Because roosts are important for social interactions and provide essential protection, it is plausible that roosts are a general and important determinant of social systems especially for foliage roosting species.

The high number and distribution of unique mitochondrial haplotypes found in this species suggests female natal dispersal. Moreover, the negative correlation between female and offspring F_{IS} as well as the frequency of female extra-pair/extra-group paternities are in line with other studies pointing to females dispersal as an inbreeding/outbreeding avoidance mechanism (*e.g.* Blomqvist *et al.* 2002, Tarvin *et al.* 2005, Muniz *et al.* 2006). The proximate mechanisms that enable *U. bilobatum* females to evaluate relatedness between themselves and potential mates are currently unknown and a possible role of MHC genes, as reported in other mammals (Piertney & Oliver 2006) remains speculative.

Tent-roosting bats have become a keystone species in forest fragments because they can be the last remaining dispersers of medium and large seeds in small forest patches (*e.g.* Melo *et al.* 2009). However, Peter's tent-roosting bat appears to have developed higher preferences for roosting in introduced plants, such as *C. nucifera* (Chan & Elevitch 2006, Baudouin & Lebrun 2009, Sagot *et al.* submitted). When using this plant species, social groups exhibit higher relatedness compared to groups roosting in different plant species. Since coconut palms are found mainly in human-modified habitats, the direct interaction that Peter's tent-roosting bats have with humans may have negative effects at the population level. A decrease in abundance or disappearance of *U. bilobatum* could have detrimental effects on forest fragments, where other large seed dispersers are absent. Thus, understanding dispersal behavior and social structure, especially in human-modified habitats, is extremely important in determining persistence, and hence optimal management strategies. Strategies including information on social behavior and demographics will be able to assure long-term survival of subpopulations or small populations. My study provides important information on the ecological and microevolutionary patterns affecting cohesion and stability of social structure and

will help inform conservation and management strategies directed toward maintaining stable populations.

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CHAPTER 4. THE EVOLUTION OF GROUP STABILITY AND ROOST LIFESPAN: PERSPECTIVES FROM TENT-ROOSTING BATS[1]

INTRODUCTION

Group formation in animal societies has been studied intensively in many taxa. Numerous strategies such as parental care and delayed juvenile dispersal influence group formation and ultimately affect stability of social behavior within groups (Michener 1958, Reeve & Keller 1995, Langer *et al*. 2004, Van Horn *et al.* 2007). Bats stand out among mammals because of the high number of species that are gregarious and social (Kerth 2008) and the diversity of mating systems they possess (Bradbury 1977, McCracken & Wilkinson 2000). Knowledge about bat social and mating systems is, however, meager, even for the small proportion of species that have been studied in detail (McCracken & Wilkinson 2000, Kunz & Lumsden 2003).

Kerth (2008) proposed that longevity combined with philopatry could reinforce the formation of stable social groups in bats, which at the same time promotes cooperation. Nonetheless, because bat species utilize different habitats, resources and roost types, distinctive ecological, behavioral and evolutionary pressures may influence group formation and sociality. For example, tent-roosting bats possessing adaptations for modifying natural structures may more readily encounter potential roosts, but may also be negatively impacted by greater exposure to predators such as snakes, raptors and monkeys (Boinski & Timm 1985) relative to bats that utilize preexisting and more permanent refuges. Moreover, these species may benefit from group living because members can cooperate in roost construction (Rodriguez-Herrera *et al*. 2006, 2008, Alcock 2009).

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Thus, roost type and lifespan may have influenced group stability in bats over evolutionary time. Although benefits from cooperation especially in roost use may be important in maintaining social groups (Alcock 2009), such a hypothesis has not been evaluated for tent-roosting bats.

In the tropics, there are at least twenty-two species of bats that use modified plant structures as tents. Seventeen species belong to Phyllostomidae, one to Vespertilionidae and four to Pteropodidae (Kunz *et al.* 1994, Kunz & Lumsden 2003). Some of these bats may have evolved body masses or particular tooth shapes that promote modification or construction of tents in specific plant species (Kunz & Lumsden 2003). Because tent-roosting bats build their own roosts in plants with particular architectures, they may be more limited by roost availability than other foliage-roosting bats. In contrast, tent-roosting bats may be less limited than species that use permanent roosts such as caves and tree holes because plant roosts are likely more abundant than tree holes and cave roosts in many systems. These traits make tent-roosting bats an interesting group to evaluate causes and consequences of sociality.

Most tent-roosting bats have polygynous mating systems (McCracken & Wilkinson 2000). In some species, social groups can be considered stable in the sense that individuals stay together for long periods of time while in other species groups are less stable and individuals may change groups even on a daily basis (Rodriguez-Herrera *et al.* 2006, Chaverri & Kunz 2006, Campbell 2008, Chaverri *et al.* 2008). This difference in group stability may be related to the plant species selected for tent construction. Bats using tents that persist for long periods of time, such as kitul (*Caryota urens*) or coconut palms, (*Cocos nucifera*) (Rickart *et al.* 1989, Timm & Lewis 1991, Storz *et al.* 2000, Hodgkinson *et al.* 2003) usually have multiple tents that are in

good condition and available for extended periods in a particular area (*i.e.,* many vacant, available tents). Individual bats often move among these tents, reoccupying them at later times. In contrast, abundance of less persistent tents is lower and tent makers using these tents usually remain with the same group longer (*i.e.,* Rodriguez-Herrera *et al.* 2008, B. Rodriguez-Herrera pers. comm). Because different plant species used for tent construction have different morphological and ecological characteristics such as leaf or stem hardness, spatial distribution, availability and lifespan, use of plants with different characteristics may have played an important role in the evolution of social living in tent-roosting bats.

If roost lifespan (time that a roost remains habitable) influences how long members of a group remain together (*i.e.,* group longevity) and ultimately the cohesiveness of female groups (*i.e.,* group stability), it can do so in two different ways: (1) constant roost switching may promote longer-lasting, more cohesive groups of females because of the need to collaborate often in roost quest and construction. Constant collaboration and formation of strong bonds between individuals will reward effort associated with roost searching and construction. It may also promote development of cooperative behaviors (Ferriere & Michod 1996, Suzuki & Akiyama 2005). Under the same scenario, use of roosts of long lifespan may require less of an energetic investment and thus may not facilitate stability of groups. An infrequent energetic investment in roost construction may reduce the necessity for individuals to interact with other members of the group. (2) Roosts of long lifespan provide more stable protection once they are built or encountered. Thus, organisms may aggregate to defend such a resource, which facilitates formation of long-lasting groups with cohesive females. Similarly, species that use roosts of short lifespan should have short-lasting group membership (groups remain together for short periods) because switching roosts often may cause constant group disintegration. To these ends,

my objective is to test whether there is correlated evolution between roost lifespan and stability and longevity of social groups in tent-roosting bats.

MATERIALS AND METHODS

LITERATURE SEARCH.— I conducted a Web of Knowledge literature search (on 20 May 2009) for publications on social systems of tent-roosting bats using the following key words: tent-making bats, tent-roosting bats, bats, mating systems, social systems and roosting ecology. I also included the names of species confirmed (by at least two independent observations) to engage in tent making or roosting behavior. Data on tent architecture and lifespan were obtained from Kunz and Lumsden (2003) and by a Web of Knowledge search for species known to use tents, using the same key words that I used for social systems. Social systems were classified into binary discrete characters based on group stability (cohesion of females) and group longevity (time the whole group remains together). This classification was based on McCracken and Wilkinson (2000) and was coded according to the predominant breeding system of each species found in the literature. Group stability was divided into (1) stable: group of females that remain in the same group longer than tent lifespan; and (2) unstable: females that remain in the group for periods shorter than tent lifespan. Group longevity was divided into (1) groups that remain together for more than a year (year-round groups); and (2) groups that remain together less than a year (seasonal groups). Tents were also coded into binary discrete characters for analyses based on their lifespan. Because bats using tents made in herbaceous plants and other soft structures tend to exhibit a different social system (McCracken & Wilkinson 2000) compared to bats that use palms or other long lasting tents, I decided to separate these plants in two different categories. Tent lifespan was assumed to be short for tents made in species of monocots, or

herbaceous plants such as *Piper* spp. because they typically become inhospitable within one to six months after first observation (M. Sagot, pers. obs). Tent lifespan was assumed to be long in bats that use palms and other plant species where tents last for a year of more. A tent lifespan was assigned to every bat species. Designation was based on at least three independent observations of bat groups using particular plant species in places where the tent maker was the only or one of a few tent-roosting bat species present. This assures that tents used were likely built by that bat species. I found suitable data for fifteen of the twenty-two species of bats that construct tents (*Artibeus jamaicensis, Artibeus lituratus, Balionycteris maculata, Cynopterus brachyotis, Cynopterus horsfieldii, Cynopterus sphinx, Dermanura cinerea, Dermanura phaeotis, Dermanura watsoni, Ectophylla alba, Rinophylla pumilio, Vampyressa nymphaea, Vampyressa thyone, Uroderma bilobatum* and *Uroderma magnirostrum*).

ANALYTICAL APROACH.— If there is a correlation between roost lifespan and group stability or longevity, the evolutionary order of events may have occurred in any of three different directions: (1) a change in roost type evolved first, producing a change in group stability and longevity; (2) the evolution of a particular group stability and longevity occurred first, causing a change in roost use; or (3) there was no particular order in the evolution of characters. These three possibilities can be distinguished by comparing specific transition rate parameters from maximum likelihood analysis. In contrast, if roost lifespan had little or no influence on group stability and longevity, I expected to find independent evolution of characters across the phylogeny.

To test my hypotheses, I reconstructed phylogenetic trees and traced ancestral states using Bayestraits (Pagel 2007) and Mesquite version 2.74 (Maddison and Maddison). I used the

supertree published by Jones *et al.* (2005) trimmed to comprise the fifteen selected taxa to estimate the phylogenetic relationship among species. This supertree was ideal because it contains all tent-roosting bats species and has branch lengths estimating degree of divergence. To test the hypothesis of correlated evolution between group stability, group longevity and roost lifespan, I used Pagel's (1994) method for comparative analysis of discrete characters using the Discrete module in BayesTraits (Pagel 2007) and Pagel94 module in Mesquite 2.01 (Maddison and Maddison). This method applies a continuous time Markov model of trait evolution that allowed testing of the correlated evolution hypothesis by fitting data to two maximum likelihood models: (1) a model of independent evolution where one trait evolves independently of the state of the other trait; and (2) a model of dependent evolution where the rate at which one trait evolves is dependent on state of the other trait. The independent model has four transition parameters, two forward (α_1 and α_2) and two backward (β_1 and β_2). The dependent model has eight parameters (q_{ij}) with each possible transition from state *i* to *j*. This test is called the omnibus test (Pagel 1994). The omnibus test returned the log-likelihood (lnL) for the independent and dependent models. I then conducted a Likelihood Ratio (LR) test using LR= 2(log-likelihood[Dependent model)–log-likelihood[Independent model]). This LR value is usually distributed as a chi-square with four degrees of freedom (Pagel 1994) and a LR $\geq$ four are conventionally considered evidence that one model explains data significantly better than the other (Pagel 1999). Small phylogenies or phylogenies with small amounts of variation in the tips, as in mine, tend to produce LR's distributed with fewer degrees of freedom. In these cases it is recommended that a null distribution be simulated (Pagel 1994, Pagel 1997). I simulated the null expectation 1000 times to create a distribution following Goldman (1990) and Pagel (1994). If I detected correlated evolution I conducted tests of conditional evolution and temporal order of

evolution of traits (Pagel 1994). I estimated the likelihood ratio of a restricted model where one transition parameter was forced to be equal to another parameter and compared this to the full or dependent evolution model of correlated evolution. For example, to test if stable groups of females are more likely to evolve in bats that use roosts of short lifespan, I forced q_{12} (the transition from unstable to stable groups of females when roost lifespan is short) and q_{34} (the transition from unstable to stable groups of females when the roosts have long lifespan), to have an equal value. I then compared the likelihood of this model to the dependent evolution model. I also tested whether each parameter was significantly different from zero by forcing each to be zero and comparing this restricted model to the full model of dependent evolution with a likelihood ratio test. This ratio was compared to a chi-square distribution with one degree of freedom. I conducted additional analyses where I controlled for body mass and correlations were still significant (results not shown). Polytomies were arbitrarily resolved using the Mesquite random polytomy resolution function. I repeated tests 100 times using 100 different randomly resolved trees and this did not qualitatively affect results (results not shown).

RESULTS

My literature review returned complete data on tent lifespan, group stability and group longevity for fifteen species in eight genera belonging to two families and two suborders (Fig. 4.1). Three of five species that use tents of short lifespan exhibited stable groups of females. Species that contrasted with this pattern were *D. cinerea* and *R. pumilio* (Fig.4.1A). All ten species that use tents of long lifespan had unstable groups of females. Data on group longevity also supported the hypothesis that tent lifespan is associated with stable social systems. All ten species using tents of long lifespan demonstrated seasonal groups and four of five species with tents of short

lifespan had year-round groups. The species that contrasted with this pattern was *D. cinerea* (Fig. 4.1B).

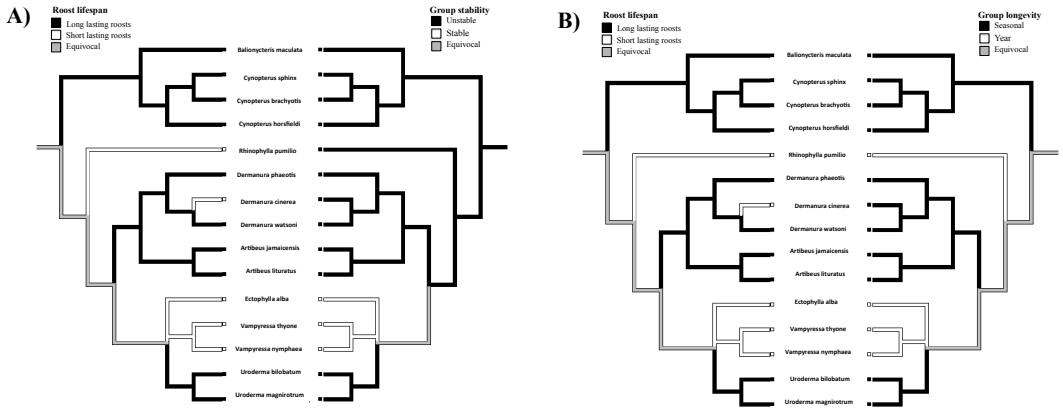

FIGURE 4.1. Mirror trees showing correlation between group stability, group longevity and roost lifespan. Character states were traced over a phylogeny of tent-roosting bats. Trees were created in Mesquite 2.74 (Maddison & Maddison), using parsimony and maximum likelihood. The phylogeny is based on Jones et al. (2005). Group longevity was divided into year-round groups and seasonal groups. Group stability (cohesion of females) was divided into stable and unstable group of females. **(A)** Correlation between group longevity and roost lifespan. **(B)** Correlation between group stability and roost lifespan. Character states where taken from: Kunz & Lumsden (2003), Hodgkinson & Kunz (2006), Hodgkinson *et al.* (2003), McCracken & Wilkinson (2000), Campbell (2008), Campbell & Kunz (2006), Storz *et al*. (2000), Storz & Kunz (1999), Machado *et al.* (2008), Timm (1987), Ortega *et al.* (2003), Ortega & Castro-Arellano (2001), Ortega & Arita (2000), Muñoz-Romo (2006), Tamsitt & Valdivieso (1965), Timm (1985), Chaverri *et al*. (2008), Chaverri & Kunz (2006), Rodriguez-Herrera *et al.* (2008), Rodriguez-Herrera et al. (2006), Timm (1982), Henry & Kalko (2007), Rinehart & Kunz (2006), Charles-Dominique (1993), Kunz & McCracken (1996), Lewis (1992), Timm & Lewis (1991), Baker & Clark (1987), Brooke (1987), Timm (1984), Zortéa & Ferreira Alves de Brito (2000), Lewis & Wilson (1987).

Maximum likelihood analysis indicated that evolution of tent lifespan and group stability is correlated such that female groups were stable in lineages with tents of short lifespan. The dependent model fit the data better than the independent model (-13.95 vs. -9.94, $P < 0.05$; Table 4.1). I also found that evolution of tent lifespan and group longevity was correlated; year-round groups use tents of short lifespan. Likelihood of the independent model was -14.91 and the

dependent model was -8.93 ($P < 0.05$; Table 4.1). There was no evidence that evolutionary transitions from unstable to stable groups of females or year-round to seasonal groups tend to occur in species that use tents of short lifespan (Table 4.1). One transition rate parameter was significantly different from zero for the correlation between group stability and tent lifespan (q_{31}; Fig. 4.2A) and one transition (q_{21}) was significantly different from zero for the correlation between group longevity and tent lifespan (Fig. 4.2B). I also found no evidence for temporal order in evolution between group stability and group longevity with tent lifespan (Table 4.1).

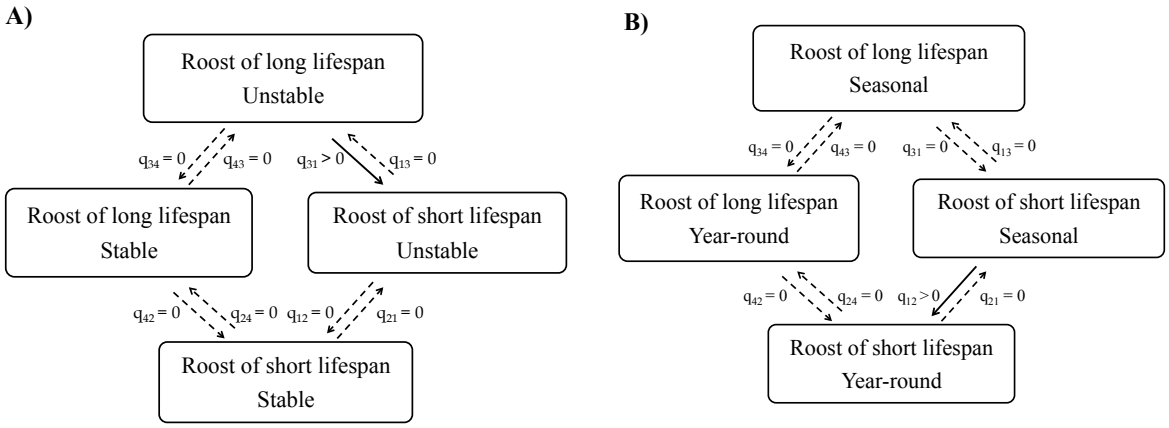

FIGURE 4.2. Flow diagrams of transition rate parameters involved in evolution of group stability and longevity relative to lifespan of the roost. 'Short lasting' refers to roosts constructed in plant species of short duration such as herbaceous and monocots while 'long lasting' refers to roosts that persist longer such as palms. Transition rate parameters are denoted by q_{ij}. Subscripts indicate character states at beginning (*i*) and end (*j*) of a given transition. In this correlated evolution model there are four possible state combinations 1 (0,0), 2(0,1), 3 (1,0) and 4 (1,1). Dotted arrows represent pathways that are not significantly different from zero. **(A)** Transition rate parameters for evolution of group stability. 'Stable' refers to group of females that stay together with the same group for long periods of time while 'unstable' refers to group of females that switch roosts on a daily basis. Transition q_{31} was different from zero, indicating the most likely evolutionary path transition. **(B)** Transition rate parameters for group longevity relative to lifespan of the roost. 'Year-round groups' refers to groups that stay together for more than a reproductive season while 'seasonal groups' refers to groups that stay only for a reproductive season or less. Transition q_{12} was different from zero, indicating the most likely evolutionary path transition.

TABLE 4.1. Hypothesis tests between group stability (stable and unstable group of females) and group longevity (year-round and seasonal groups) and roosts lifespan (long and short lifespan).

	Hypothesis	Test	LR	P
Group stability	Correlated evolution between female fidelity and roost lifespan L(D) > L(I)	L(I) ≠ L(D)	8.02	<0.05*
	Change to stable group of females depends upon use of roosts of short lifespan $q_{12} > q_{34}$	$q_{21} \neq q_{43}$	-0.08	>0.05
	Change to unstable group of females depends upon use of roosts of long lifespan $q_{21} > q_{43}$	$q_{12} \neq q_{34}$	-0.12	>0.05
	Change to use of roosts of short lifespan depends upon stable group of females $q_{13} > q_{24}$	$q_{42} \neq q_{31}$	-0.08	>0.05
	Change to use of roosts of long lifespan depends upon stable group of females $q_{31} > q_{42}$	$q_{24} \neq q_{13}$	0.00	>0.05
Group longevity	Correlated evolution between group longevity and roost lifespan L(D) > L(I)	L(I) ≠ L(D)	11.96	<0.05*
	Change to year-round groups depends upon use of roosts of short lifespan $q_{12} > q_{34}$	$q_{21} \neq q_{43}$	0.00	>0.05
	Change to seasonal groups depends upon use of roosts of long lifespan $q_{21} > q_{43}$	$q_{12} \neq q_{34}$	-0.3	>0.05
	Change to use of roosts of short lifespan depends upon year-round groups $q_{13} > q_{24}$	$q_{42} \neq q_{31}$	-0.08	>0.05
	Change to use of roosts long lifespan depends upon seasonal groups $q_{31} > q_{42}$	$q_{24} \neq q_{13}$	-0.08	>0.05

* Significant values

DISCUSSION

Correlated evolution between group stability or group longevity and tent lifespan in tent-roosting bats provides insights into the variety of harem-based social systems common in this group. As demonstrated by this study, most bats that used short lasting tents also had stable groups, and

most species that used long lasting tents had unstable groups, suggesting that group stability and tent lifespan did not evolve independently. Also, most species with year-round groups often used tents of short lifespan, which is also consistent with the hypothesis that group longevity was correlated with roost lifespan. Species that did not exhibit such a pattern were *D. cinerea* and *R. pumilio.* I was unable to explain this. It is possible that a lack of detailed information on these species led to a misclassification of their social system. Indeed this is the first phylogenetically-controlled statistical assessment in tent-roosting bats of patterns of group stability, longevity and tent lifespan and these results overall suggest that the particular historical mechanism generating such patterns resulted in the correlated evolution of these characteristics.

Using existing patterns like those described here to propose working hypotheses on how a correlation between tent lifespan and either group longevity or group stability may arise may stimulate further research that can potentially enhance understanding of these complex mating systems. Moreover, further investigation characterizing social systems and roost preferences, especially within an evolutionary context, will add to our understanding of correlated evolution of these distinctive behavioral characteristics.

WHY DO GROUP STABILITY AND ROOST LIFESPAN EVOLVE TOGETHER?— Multiple hypotheses have been proposed to explain group formation and sociality (Alexander 1974, Barta & Szép 1992, Avilés 1999, Trivers 2002, Safi & Kerth 2007, Alcock 2009). These hypotheses, however, are of limited utility in explaining causes of sociality in tent-roosting bats (Kunz & Lumsden 2003). In this group of bats, stable and complex social interactions should be favoured if cooperation reduces per-individual costs of roost construction and maintenance. Species such as *E. alba* spend approximately one week constructing a tent (Rodriguez-Herrera *et al.* 2006) which lasts from three to six weeks on average (Rodriguez-Herrera *et al*. 2006). Therefore, a single

group spends approximately 122 days a year constructing tents. Due to large time and energy investment in tent construction, groups may remain together year-round. This may be to share the cost of building tents and avoid increased *per capita* energy expenditure. These costs can be incurred by joining new groups that are in the process of constructing new tents, especially if they switch groups often. Sharing tasks such as plant search and tent construction may enhance social bonds among individuals because it facilitates long-term interactions and can promote cooperative behaviors. On the other hand, in species that use long-lasting tents, such as *C. sphinx,* individuals spend approximately 30–50 days on tent construction that is usually undertaken by a single bat (Balasingh *et al.* 1995). These groups usually have unstable membership and groups form seasonally.

Complex and stable social interactions in tent-roosting bats that use tents of short lifespan can be found in species such as *E. alba* (Rodriguez-Herrera *et al.* 2006, Rodriguez-Herrera *et al.* 2008) and *V. thyone* (Zortea *et al.* 2000) where the number and membership of individuals in groups is usually stable and independent of presence of other social groups nearby. On the other hand, in species that use tents of long lifespan such as *D. watsoni* (Chaverri *et al.* 2008), *U. bilobatum* (M. Sagot, unpubl. data) and members of *Cynopterus* (Campbell 2008), females in particular switch tents and social groups and group composition changes even on a daily basis. This is also the case for species like the white-throated round-eared bat (*Lophostoma silvicolum;* Dechmann *et al.* 2007) that uses termite nests as roosts, suggesting that cooperation may not be relevant in bats with roosts of long lifespan. Moreover, observed specificity in the use of particular tent styles and plant species for tent construction (Kunz & Lumsden 2003, Campbell 2008, Rodriguez-Herrera *et al.* 2008, M. Sagot, pers. obs) suggests that ability to construct particular tent architectures in specific plant species (resulting architectures are more a

consequence of leaf shape than behavioral repertoire of bats) is an intrinsic characteristic of each tent-roosting bat species. This specificity may be determined by morphological and behavioral characteristics (Kunz & Lumsden 2003). Therefore, I hypothesize that adaptations in ecology, behavior and morphology in bats that enhance construction of tents of short lifespan also promote cooperation and ultimately may have lead to formation of stable social groups.

SINGLE OR MULTIPLE PATHWAYS TO EVOLUTION OF SOCIAL SYSTEMS.— For group stability and group longevity, rate parameters q_{31} and q_{12} respectively, were greater than zero. Values greater than zero contribute more to the lnL and usually indicate the most likely evolutionary path (Pagel 1994). I found no consistent pattern, however, to the particular evolutionary order of characters across the phylogeny. Lack of evidence for temporal order suggests that evolution of group stability and group longevity with roost lifespan could occur simultaneously suggesting that social behavior may change on ecological rather than evolutionary time scales. Moreover, phylogenetic methods may be unable to detect presence of more than one change in a trait between nodes in a phylogeny (Olson *et al.* 2009), which further complicates interpretation. Individuals of the same species can exhibit plasticity in their behavior, eliciting different behaviors suitable for different environmental conditions (West-Eberhard 2003). Differences in mating system based on type of roost have been reported for species such as *A. jamaicensis* (Morrison 1978, Kunz *et al.* 1983), and such plasticity could be the case for many tent-roosting bats. They are capable of modifying their social system, roost selection, or both in different environments to enhance fitness (Kunz 1982, Fleming 1986, Fleming *et al.* 1987, Brooke 1990, Frank 1998, Swartz *et al.* 2003, Chaverri *et al.* 2007, Campbell 2008). Moreover, abundance and availability of plant species used for tent construction in habitats where these bats feed may limit

selection to these particular plant species or tent architectures as well as place an upper bound on number of bats per group and number of groups able to inhabit a particular habitat (Chaverri & Kunz 2006, Chaverri *et al.* 2007, Campbell 2008, Chaverri *et al.* 2008, Rodriguez-Herrera *et al.* 2008). For these reasons, without clear evidence to the contrary, it is reasonable to suspect that changes in group stability and group longevity in tent-roosting bats are influenced by ecological characteristics such as plant availability and distribution and can change rapidly and even at multiple times across a phylogenetic branch, making it difficult to detect the direction of causal change in the evolution of characters.

Many hypotheses have been proposed to explain group formation and evolution of sociality in bats (Kerth 2008). Little attention has been paid to species with complex roosting behaviors like tent-roosting bats. Demonstration of correlated evolution between group stability and longevity with tent lifespan is an essential step toward understanding causes and consequences of sociality. The lack of order in the evolution of characters across the phylogeny suggests that although tent lifespan may have influenced social bonds in tent-roosting bats, the evolutionary path differs among species and may be influenced by ecological factors such as diet, specialization, tent availability and tent distribution. The ability to identify how roost lifespan can interact with other ecological processes to produce complex behaviors may provide the basis for understanding the variety of mechanisms that interact to produce the diversity of social systems in Chiroptera.

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CHAPTER 5: CONCLUSIONS

CONCLUSIONS

It is widely known that ecological and environmental factors (*e.g*. habitat) have important implications to social living (Chaverri & Kunz 2010). Although these factors are constantly changing in predictable and unpredictable ways (Wingfield 2003), little effort has been made to disentangle habitat effects on social structure in variable environments. Thus, this study aimed to investigate habitat characteristics that influenced not only the distribution but also the evolution of social systems in tent-roosting bats, under relatively pristine and human-modified environments. This group of bats is formed by species of divergent evolutionary origins but similar roosting habits, suggesting convergence in the use of these structures (Kunz *et al.* 1994).

In Chapter 2 (Sagot *et al.* submitted), I presented the first study to examine the influence of habitat at two different spatial scales (macrohabitat and microhabitat) on the distribution and density of *U. bilobatum*. I found that both macrohabitat and microhabitat scales explained presence and density of *U. bilobatum*. However, microhabitat scale, particularly presence of coconut palms (*Cocos nucifera*), had the highest unique predictive power. *U. bilobatum* preferentially inhabits areas with high density of coconut palms and rarely uses native plants in the forest. These palms were introduced recently in the Neotropics and are found only in human-modified areas, mostly planted as agricultural crops or ornamentals. Therefore, I hypothesized that *U. bilobatum* is expanding its range into these areas following the expanded distribution of this exotic plant species.

Differences in abundance of bats between forest and human-modified habitats have direct consequences on the adult sex ratios (Hamilton 1967), male and female reproductive strategies (Clutton-Brock 1991) and reproductive success (Clutton-Brock 1988). Consequently, it is

reasonable to propose that group cohesion and stability in *U. bilobatum,* changes depending on the habitat and plants species used for tent construction. Thus, to better understand consequences of habitat use on group stability and cohesion, in Chapter 3, I described the overall genetic structure of *U. bilobatum*. Then, I combined this information with habitat characteristics to better understand the effects of habitat on their social system. I found that *U. bilobatum* had little genetic structure across different geographical levels. After dividing the analyses by age and gender, I determined that adult females were more structured than adult males and offspring. Moreover, unique mitochondrial haplotypes were shared among different regions, suggesting female natal dispersal. Female dispersal appeared to be related to inbreeding avoidance. Additionally, habitat variables explained 80% of the variation in group relatedness. Roost characteristics again contributed more to the explained variation. This pattern was driven by relatedness of adult females within social groups, suggesting that females using roosts of specific characteristics exhibit higher relatedness. Thus, I concluded that roost characteristics are the most important determinants of group stability and cohesion in *U. bilobatum*.

Aside from *U. bilobatum,* there are at least 23 other bat species that utilize modified plants as roosts (Kunz & Lumsden 2003). In some species, social groups are stable while in others individuals change groups even on a daily basis (Timm 1984, Rickart *et al.* 1989, Brooke 1990, Timm & Lewis 1991, Storz *et al.* 2000, Hodgkinson *et al.* 2003, Rodríguez-Herrera *et al.* 2006). Because different plant species used for tent construction have different morphological and ecological characteristics such as leaf or stem hardness, spatial distribution, availability and lifespan, use of plants with different characteristics may have played an important role in group stability and cohesion in tent-roosting bats. Therefore, in Chapter 4 (Sagot & Stevens 2012), I tested correlated evolution of group stability and group longevity with tent lifespan using a

phylogenetically-controlled method for discrete characters (Sagot & Stevens 2012). I found that group stability and group longevity are correlated with tent lifespan. Most bats that used tents of short lifespan also had stable groups, and most species that used tents of long lifespan had unstable groups, suggesting that group stability and tent lifespan did not evolve independently. Likewise, most species with year-round harems often used tents of short lifespan, which is also consistent with the hypothesis that group longevity was correlated with roost lifespan. Thus, since roosts have significant influence on fitness and survival in bats, I proposed that they are the most important determinants of group cohesion and stability in tent-roosting bats.

Subdivision of groups in cohesive social systems is conducive to the evolution of cooperative and altruistic behaviors that promote rapid microevolutionary changes and shifts in allelic frequencies (Storz *et al.* 2001). This is because levels of genetic differentiation among adjacent social groups can sometimes exceed that between more inclusive, geographically defined subdivisions of a population (Storz 1999). Thus, studying the evolution of group formation and cohesion will add important information to our knowledge of evolution.

Group formation, size and cohesion have important effects on population growth rates, susceptibility to diseases, response to habitat exploitation, population recovery and patch recolonization (Dobson & Poole 1998). Still, conservation biologists have been primarily interested in behavior at broader scales (*e.g.* populations and species) and have almost disregarded the importance of group formation and living (Dobson & Poole 1998, Eadie *et al.* 1998). This is especially true for small mammals (Brock & Kelt 2004). In bats for example, lack of information and education about their habitat and ecology has caused people to believe that they are harmful. Furthermore, multiple species have habituated to live in or close to human habitats (Kunz & Lumsden 2003). Consequently, people that live in areas close to forests where

bats are more abundant try to eradicate those that roost near their homes. The direct interaction these species have with humans may have negative effects at the population level. The Peter's tent-roosting bat, *U. bilobatum* is becoming more abundant in human-modified habitats because of their use of non-native coconut palms (Timm & Lewis 1991, Lewis 1992, Sagot *et al.* submitted). However, little effort has been done to understand their roosting ecology and behavioral characteristics in response to this recent habitat switch. A radical change in abundance of *U. bilobatum* could have detrimental effects to forest fragments, especially those lacking seed dispersers. Therefore, I suggest strong prioritization of conservation strategies, especially through education. Taking advantage of the environmental education programs that many national parks and protected areas have with local schools will be extremely important to educate people, especially children, about bats living in their neighborhoods and their importance to the environment. I also encourage local bat conservation programs to prioritize their activities in such areas.

For many years, research on inclusive fitness (first proposed by Hamilton 1967) monopolized hypotheses on group formation and stability. My results revive the realm of variable ecological factors in the evolution and stability of social systems. The observed relationships between roosting ecology, group cohesion and stability in tent-roosting bats suggest that these roosts play an important role in the evolution of group formation. Incorporating ecological and environmental factors in the study of sociality under current habitat configurations, will allow broad understanding of forces that bring together individuals into cohesive social groups. Moreover, it provides further predictions on how human impacts to the landscape will affect persistence of natural populations.

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APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2

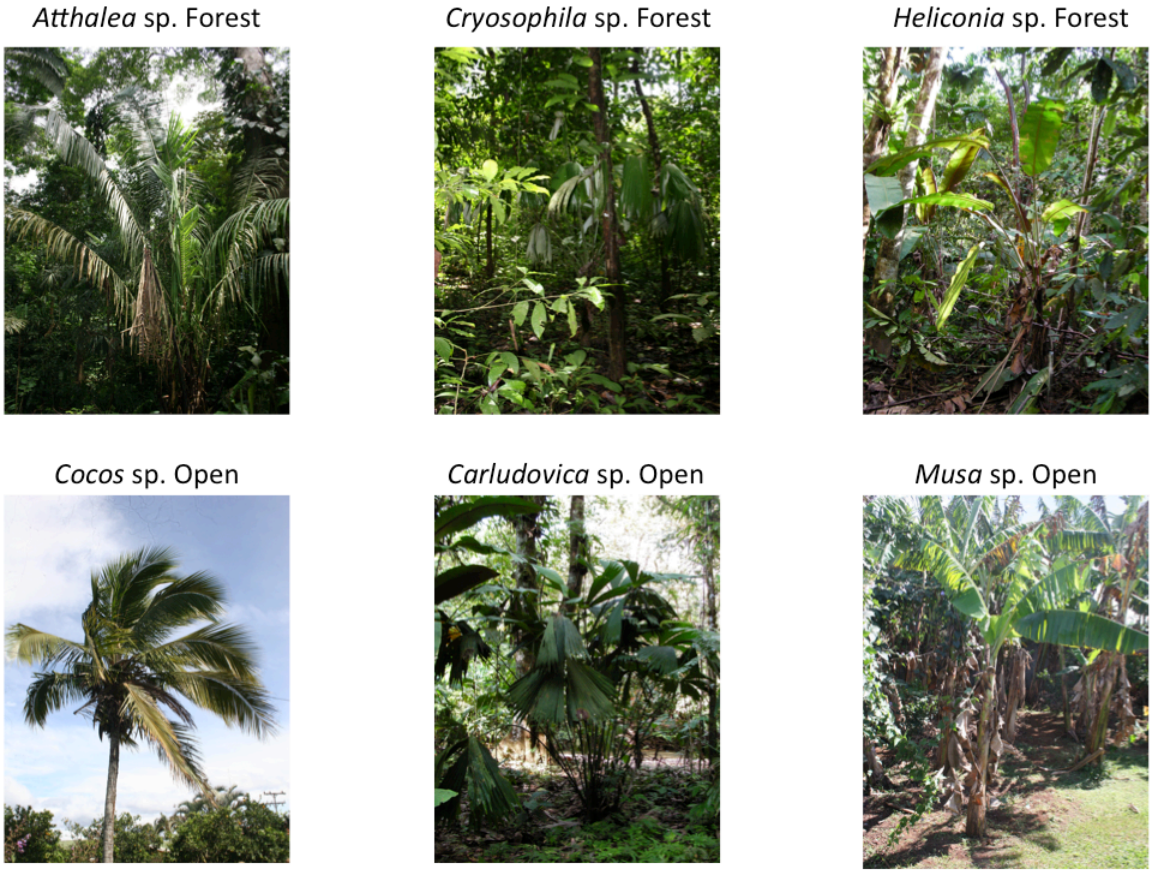

FIGURE A.1. Similarity among plant species in forest and human-modified areas, commonly used for tent construction by *U. bilobatum*.

HERBARIA CONSULTED FOR DISTRIBUTION OF *ATTALEA* SPP

Royal Botanic Gardens, Kew, Missouri Botanical Garden, Instituto de Ciencias Naturales, Nationaal Herbarium Nederland - Leiden, United States National Plant Germplasm System Royal Museum of Central Africa - Metafro-Infosys - Xylarium, The AAU Herbarium Database, Herbarium Berolinense, Andes to Amazon Biodiversity Program, Botany (UPS), IIAPPoa, Phanerogamie, Herbario UNAP, Botanical Museum, Copenhagen. Real Jardin Botanico (Madrid), Vascular Plant Herbarium (MA), Fairchild Tropical Botanic Garden Virtual

Herbarium Darwin Core format, NMNH Botany Collections, Fundación Miguel Lillo Provider, Phanerogamic Botanical Collections (S), RBGE Herbarium (E), Herbarium of The New York Botanical Garden, MEXU/Flora de Oaxaca, RBGE Living Collections, Rapid Assessment Program (RAP) Biodiversity, SysTax, The AAU PalmTransect Database, Herbier de la Guyane, Biodiversidad de Costa Rica, Paleobiology Database, Peabody Paleobotany DiGIR Service, Peabody Paleoportal DiGIR Service (PB).

HERBARIA CONSULTED FOR DISTRIBUTION OF *CRYOSOPHILA* SPP.

Herbario, Missouri Botanical Garden, United States National Plant Germplasm System Collection, Andes to Amazon Biodiversity Program, Fairchild Tropical Botanic Garden Virtual Herbarium Darwin Core format, SysTax, Herbario del Instituto de Ecología, A.C., México (IE-BAJIO), Herbario del Instituto de Ecología, A.C., México (IE-XAL), Herbarium Berolinense, NMNH Botany Collections, Phanerogamic Botanical Collections (S), RBGE Herbarium (E), Instituto de Ciencias Naturales, MEXU/Flora de Oaxaca, RBGE Living Collections, Royal Botanic Gardens, Kew, Herbario XAL del Instituto de Ecología, A.C., México (IE-XAL), Herbario IEB del Instituto de Ecología, A.C., México, Biodiversidad de Costa Rica, Paleobiology Database, The AAU Herbarium Database, Colección de Monocotiledóneas Mexicanas (UAM-I).

TABLE A.1. Plant taxa, number of tents, number of bats and geographic coordinates of tents in Carara and Sarapiquí, Costa Rica.

Plant taxa	Number of tents	Number of bats	UTM(16) X	UTM(16) Y
Attalea rostrata	10	0	762994	1081356
Attalea rostrata	9	0	762661	1081105
Attalea rostrata	8	0	762434	1081001
Attalea rostrata	8	0	762436	1081142
Attalea rostrata	7	0	762432	1081140
Attalea rostrata	7	0	762442	1081173
Heliconia spp.	5	0	763044	1081244
Attalea rostrata	5	0	762869	1081158
Attalea rostrata	5	0	762450	1081207
Attalea rostrata	5	2	762679	1081107
Attalea rostrata	4	0	762675	1081634
Attalea rostrata	4	0	762896	1081176
Attalea rostrata	4	0	762950	1081339
Attalea rostrata	4	0	762597	1081677
Attalea rostrata	4	0	762443	1081154
Attalea rostrata	4	0	762469	1081201
Cryosophila guarara	4	0	763931	1083951
Attalea rostrata	4	4	763811	1083972
Heliconia spp.	3	0	763041	1081266
Carludovica spp.	3	0	762648	1081582
Attalea rostrata	3	0	762589	1081059
Attalea rostrata	3	0	762365	1081026
Attalea rostrata	3	0	762346	1081041
Attalea rostrata	3	0	762572	1081188
Attalea rostrata	3	0	762722	1081120
Attalea rostrata	3	0	763036	1083435
Cryosophila guarara	3	0	764015	1083953
Attalea rostrata	3	0	763592	1084100
Heliconia spp.	2	0	763023	1081253
Attalea rostrata	2	0	762694	1081661
Carludovica spp.	2	0	763143	1081483
Attalea rostrata	2	0	762669	1081113
Attalea rostrata	2	0	762493	1081013
Attalea rostrata	2	0	762381	1081019
Attalea rostrata	2	0	762353	1081010
Attalea rostrata	2	0	762408	1081158
Attalea rostrata	2	0	762428	1081171
Carludovica spp.	2	0	767356	1078582

Cocos nucifera	2	0	763057	1083459
Attalea rostrata	2	0	764333	1084139
Attalea rostrata	2	0	763149	1083830
Attalea rostrata	2	0	763182	1083637
Heliconia spp.	1	0	762499	1081014
Attalea rostrata	1	0	762467	1081016
Attalea rostrata	1	0	762459	1081030
Attalea rostrata	1	0	762440	1081024
Attalea rostrata	1	0	762397	1081126
Attalea rostrata	1	0	762423	1081144
Attalea rostrata	1	0	762435	1081147
Attalea rostrata	1	0	762454	1081187
Attalea rostrata	1	0	762435	1081168
Attalea rostrata	1	0	762450	1081194
Attalea rostrata	1	0	762464	1081203
Attalea rostrata	1	0	762470	1081208
Attalea rostrata	1	0	762527	1081209
Attalea rostrata	1	0	762692	1081124
Carludovica spp.	1	0	767360	1078583
Carludovica spp.	1	0	767270	1078518
Carludovica spp.	1	0	767285	1078284
Carludovica spp.	1	0	767352	1078540
Carludovica spp.	1	0	767352	1078536
Carludovica spp.	1	0	767292	1078511
Carludovica spp.	1	0	767296	1078510
Carludovica spp.	1	0	767300	1078510
Carludovica spp.	1	0	767328	1078497
Carludovica spp.	1	0	767335	1078508
Carludovica spp.	1	0	767331	1078512
Carludovica spp.	1	0	767350	1078563
Carludovica spp.	1	0	767344	1078556
Carludovica spp.	1	0	767549	1078587
Attalea rostrata	1	0	763047	1083459
Attalea rostrata	1	0	763054	1083439
Attalea rostrata	1	0	763047	1083459
Attalea rostrata	1	0	763062	1083464
Cocos nucifera	1	0	763057	1083457
Cocos nucifera	1	0	763061	1083469
Attalea rostrata	1	0	763096	1083456
Attalea rostrata	1	0	763096	1083454
Attalea rostrata	1	0	763124	1083498
Attalea rostrata	1	0	763131	1083541
Musa acuminata	1	0	763284	1083872

Musa acuminata	1	0	763198	1083921
Musa acuminata	1	0	763243	1083977
Musa acuminata	1	0	763318	1083035
Attalea rostrata	1	0	763725	1083953
Cryosophila guarara	1	0	764123	1084060
Musa acuminata	1	0	764252	1084142
Attalea rostrata	1	0	764333	1084140
Attalea rostrata	1	0	764362	1084276
Attalea rostrata	1	0	764487	1084339
Attalea rostrata	1	0	764496	1084344
Attalea rostrata	1	0	764669	1084408
Attalea rostrata	1	0	764597	1084398
Attalea rostrata	1	0	764507	1084364
Attalea rostrata	1	0	764474	1084362
Cocos nucifera	1	0	764326	1084287
Attalea rostrata	1	0	763791	1083970
Attalea rostrata	1	0	763778	1083975
Attalea rostrata	1	0	763636	1084108
Attalea rostrata	1	0	763575	1084186
Attalea rostrata	1	0	763266	1083850
Attalea rostrata	1	0	763271	1083683
Attalea rostrata	1	0	763126	1083576
Attalea rostrata	1	0	763060	1083514
Attalea rostrata	1	1	764313	1084145
Attalea rostrata	1	2	763082	1083483
Attalea rostrata	1	3	762427	1081027
Attalea rostrata	1	3	764119	1083544
Attalea rostrata	1	3	763041	1083515
Attalea rostrata	1	4	764558	1084385
Attalea rostrata	1	6	763070	1083520
Cocos nucifera	0	0	763064	1083456
Attalea rostrata	14	0	766912	1078888
Cocos nucifera	7	14	760491	1079326
Cocos nucifera	7	5	765824	1077947
Cocos nucifera	7	2	769181	1076762
Cocos nucifera	6	10	761901	1079498
Cocos nucifera	6	8	771599	1077627
Cocos nucifera	6	6	766721	1078740
Cocos nucifera	6	1	766742	1076159
Cocos nucifera	6	1	766865	1076823
Cocos nucifera	6	1	761812	1079420
Cocos nucifera	6	0	771782	1077676
Cocos nucifera	5	5	766715	1078738

Attalea rostrata	5	4	766843	1078537
Cocos nucifera	5	2	766754	1076627
Cocos nucifera	5	2	765883	1077980
Cocos nucifera	5	2	760344	1080041
Cocos nucifera	5	2	764515	1086167
Cocos nucifera	5	1	771565	1077616
Cocos nucifera	5	1	764648	1085810
Cocos nucifera	5	0	760071	1078825
Cocos nucifera	5	0	764894	1086089
Cocos nucifera	4	13	769188	1076765
Cocos nucifera	4	8	771778	1077744
Cocos nucifera	4	8	771757	1077700
Cocos nucifera	4	4	771772	1077675
Cocos nucifera	4	2	766734	1076601
Cocos nucifera	4	1	766387	1076034
Cocos nucifera	4	0	767203	1075823
Attalea rostrata	4	0	767185	1075898
Cocos nucifera	4	0	766716	1076144
Cocos nucifera	4	0	771605	1077630
Cocos nucifera	4	0	765818	1077907
Cocos nucifera	4	0	761901	1079491
Cocos nucifera	4	0	760147	1078877
Cocos nucifera	4	0	760176	1078883
Cocos nucifera	4	0	764175	1087697
Cocos nucifera	4	0	764535	1086194
Cocos nucifera	4	0	771562	1083190
Cocos nucifera	3	5	767269	1075724
Cocos nucifera	3	4	771740	1077669
Cocos nucifera	3	2	771784	1077656
Cocos nucifera	3	2	765809	1077922
Cocos nucifera	3	2	764999	1086209
Cocos nucifera	3	1	760294	1080197
Cocos nucifera	3	1	760025	1081251
Attalea rostrata	3	0	766917	1078888
Cocos nucifera	3	0	766715	1078841
Cocos nucifera	3	0	766990	1078238
Cocos nucifera	3	0	767016	1076163
Cocos nucifera	3	0	767257	1075852
Cocos nucifera	3	0	769188	1076766
Cocos nucifera	3	0	771562	1077610
Cocos nucifera	3	0	771768	1077672
Cocos nucifera	3	0	765816	1077925
Cocos nucifera	3	0	760018	1081264

Cocos nucifera	3	0	762548	1084522
Cocos nucifera	3	0	764401	1087426
Cocos nucifera	3	0	764542	1086185
Cocos nucifera	3	0	764537	1086165
Cocos nucifera	3	0	764510	1086191
Cocos nucifera	3	0	764316	1086505
Cocos nucifera	2	13	766392	1076068
Cocos nucifera	2	12	766801	1076590
Cocos nucifera	2	6	766741	1076150
Cocos nucifera	2	6	766566	1076089
Cocos nucifera	2	4	766998	1078240
Cocos nucifera	2	2	771772	1077748
Cocos nucifera	2	2	764243	1087622
Cocos nucifera	2	1	767008	1076143
Cocos nucifera	2	1	767022	1076171
Cocos nucifera	2	1	767258	1075097
Cocos nucifera	2	1	766382	1076039
Cocos nucifera	2	1	762027	1079433
Cocos nucifera	2	1	760043	1081134
Cocos nucifera	2	0	766713	1078745
Cocos nucifera	2	0	767232	1075856
Cocos nucifera	2	0	767235	1075854
Cocos nucifera	2	0	767257	1075849
Attalea rostrata	2	0	767217	1075675
Cocos nucifera	2	0	767291	1075786
Cocos nucifera	2	0	767241	1075031
Cocos nucifera	2	0	767252	1075088
Cocos nucifera	2	0	766712	1076145
Cocos nucifera	2	0	766512	1076114
Cocos nucifera	2	0	766479	1076045
Cocos nucifera	2	0	766342	1076023
Cocos nucifera	2	0	766891	1076822
Cocos nucifera	2	0	769202	1076763
Cocos nucifera	2	0	770960	1076069
Cocos nucifera	2	0	771625	1077646
Cocos nucifera	2	0	771595	1077598
Cocos nucifera	2	0	771548	1077626
Cocos nucifera	2	0	771578	1077617
Cocos nucifera	2	0	771578	1077613
Cocos nucifera	2	0	771748	1077689
Cocos nucifera	2	0	771748	1077887
Cocos nucifera	2	0	762050	1079406
Cocos nucifera	2	0	761914	1079479

Cocos nucifera	2	0	761830	1079456
Cocos nucifera	2	0	760222	1080031
Cocos nucifera	2	0	760217	1080248
Cocos nucifera	2	0	760112	1080992
Cocos nucifera	2	0	760039	1081122
Cocos nucifera	2	0	760054	1081135
Cocos nucifera	2	0	760056	1081171
Cocos nucifera	2	0	760011	1081244
Cocos nucifera	2	0	759624	1081592
Cocos nucifera	2	0	759132	1082100
Cocos nucifera	2	0	759259	1082194
Cocos nucifera	2	0	759491	1082317
Cocos nucifera	2	0	760073	1078814
Cocos nucifera	2	0	760088	1078819
Cocos nucifera	2	0	762559	1084465
Cocos nucifera	2	0	764615	1086948
Cocos nucifera	2	0	764831	1086624
Cocos nucifera	2	0	764542	1086172
Cocos nucifera	2	0	764561	1086215
Cocos nucifera	2	0	764564	1086218
Cocos nucifera	2	0	764559	1086224
Cocos nucifera	2	0	764465	1086018
Cocos nucifera	2	0	764304	1086516
Cocos nucifera	2	0	764306	1086496
Cocos nucifera	2	0	771566	1083197
Cocos nucifera	1	38	762543	1084451
Cocos nucifera	1	24	760190	1078920
Cocos nucifera	1	16	766743	1076169
Cocos nucifera	1	16	760032	1081130
Cocos nucifera	1	10	760039	1081117
Cocos nucifera	1	7	771724	1077923
Cocos nucifera	1	6	766507	1076031
Cocos nucifera	1	4	766876	1079264
Cocos nucifera	1	4	771566	1077604
Cocos nucifera	1	4	760103	1081021
Cocos nucifera	1	4	760101	1081022
Cocos nucifera	1	4	760172	1078886
Cocos nucifera	1	3	760328	1080082
Cocos nucifera	1	2	766740	1078678
Cocos nucifera	1	2	767004	1076144
Cocos nucifera	1	2	767236	1076132
Cocos nucifera	1	2	771599	1077627
Cocos nucifera	1	2	771709	1077960

Cocos nucifera	1	2	760473	1079139
Cocos nucifera	1	2	760035	1081123
Cocos nucifera	1	1	767249	1076079
Cocos nucifera	1	1	766563	1076089
Cocos nucifera	1	1	762004	1079433
Cocos nucifera	1	1	760299	1080137
Cocos nucifera	1	1	760143	1081021
Cocos nucifera	1	1	760058	1081147
Cocos nucifera	1	1	760168	1078900
Cocos nucifera	1	1	762551	1084462
Cocos nucifera	1	1	764860	1086663
Cocos nucifera	1	0	766899	1078880
Cocos nucifera	1	0	766740	1078675
Cocos nucifera	1	0	766734	1078674
Cocos nucifera	1	0	766752	1077904
Attalea rostrata	1	0	766871	1077904
Cocos nucifera	1	0	766804	1076271
Cocos nucifera	1	0	767003	1076151
Cocos nucifera	1	0	767007	1076121
Cocos nucifera	1	0	767211	1075629
Cocos nucifera	1	0	767270	1075111
Cocos nucifera	1	0	767022	1075482
Cocos nucifera	1	0	767020	1075474
Cocos nucifera	1	0	766740	1076155
Cocos nucifera	1	0	766687	1076036
Cocos nucifera	1	0	766479	1076033
Cocos nucifera	1	0	766376	1075047
Cocos nucifera	1	0	766387	1076032
Cocos nucifera	1	0	766383	1076033
Cocos nucifera	1	0	767084	1076245
Cocos nucifera	1	0	769181	1076761
Cocos nucifera	1	0	769185	1076764
Cocos nucifera	1	0	769195	1076764
Cocos nucifera	1	0	769194	1076754
Cocos nucifera	1	0	771018	1076072
Cocos nucifera	1	0	771619	1077638
Cocos nucifera	1	0	771599	1077628
Cocos nucifera	1	0	771593	1077628
Cocos nucifera	1	0	771591	1077621
Cocos nucifera	1	0	771563	1077606
Cocos nucifera	1	0	771682	1077680
Cocos nucifera	1	0	771651	1077761
Cocos nucifera	1	0	771752	1077898

Cocos nucifera	1	0	771717	1077926
Cocos nucifera	1	0	765838	1077925
Cocos nucifera	1	0	765881	1077936
Cocos nucifera	1	0	761904	1079484
Cocos nucifera	1	0	761862	1079439
Cocos nucifera	1	0	760368	1079045
Cocos nucifera	1	0	760370	1079047
Cocos nucifera	1	0	760349	1079079
Cocos nucifera	1	0	760354	1079113
Cocos nucifera	1	0	760483	1079304
Cocos nucifera	1	0	760451	1079115
Cocos nucifera	1	0	760475	1079137
Cocos nucifera	1	0	760477	1079141
Cocos nucifera	1	0	760308	1079784
Cocos nucifera	1	0	760308	1079789
Cocos nucifera	1	0	760275	1079789
Cocos nucifera	1	0	760268	1079788
Cocos nucifera	1	0	760280	1079670
Cocos nucifera	1	0	760330	1080086
Cocos nucifera	1	0	760321	1080100
Cocos nucifera	1	0	760046	1080918
Cocos nucifera	1	0	760064	1081037
Cocos nucifera	1	0	760027	1081113
Cocos nucifera	1	0	760039	1081102
Cocos nucifera	1	0	760053	1081117
Cocos nucifera	1	0	760054	1081127
Cocos nucifera	1	0	760065	1081129
Cocos nucifera	1	0	760084	1081133
Cocos nucifera	1	0	760056	1081157
Cocos nucifera	1	0	760051	1081151
Cocos nucifera	1	0	760022	1081253
Cocos nucifera	1	0	760020	1081254
Cocos nucifera	1	0	760021	1081268
Cocos nucifera	1	0	760006	1081247
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Cocos nucifera	1	0	759454	1081525
Cocos nucifera	1	0	759409	1081635
Cocos nucifera	1	0	759202	1082152
Cocos nucifera	1	0	759184	1082126
Cocos nucifera	1	0	759506	1082276
Cocos nucifera	1	0	760199	1078915
Cocos nucifera	1	0	760165	1078865

Cocos nucifera	1	0	760154	1078890
Cocos nucifera	1	0	760148	1078891
Cocos nucifera	1	0	760100	1078793
Cocos nucifera	1	0	760038	1078778
Cocos nucifera	1	0	761922	1080547
Cocos nucifera	1	0	762026	1080681
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Cocos nucifera	1	0	814053	1151252
Cocos nucifera	1	0	814055	1151250
Cocos nucifera	1	0	813856	1151455
Cocos nucifera	1	0	813905	1151397
Cocos nucifera	1	0	813805	1151059
Cocos nucifera	1	0	813805	1151071
Cocos nucifera	1	0	813777	1151055
Cocos nucifera	1	0	813771	1151097
Cocos nucifera	1	0	813682	1151201
Cocos nucifera	1	0	813823	1151362
Cocos nucifera	1	0	813821	1151367
Cocos nucifera	1	0	813823	1151392
Cocos nucifera	1	0	814099	1151752
Cocos nucifera	1	0	814205	1151795
Cocos nucifera	1	0	820079	1155201
Cocos nucifera	1	0	820086	1155205
Cocos nucifera	1	0	819821	1154117
Cocos nucifera	1	0	819828	1154116
Cocos nucifera	1	0	819830	1154117
Cocos nucifera	1	0	819842	1154116
Cocos nucifera	1	0	819854	1154115
Cocos nucifera	1	0	819798	1154121
Cocos nucifera	1	0	819823	1154241
Cocos nucifera	1	0	820200	1155014
Cocos nucifera	1	0	820207	1155035
Cocos nucifera	1	0	818388	1151442

Cocos nucifera	1	0	818420	1154176
Cocos nucifera	1	0	818715	1155204
Cocos nucifera	1	0	818851	1155361
Cocos nucifera	1	0	819177	1153232
Cocos nucifera	1	0	819178	1153233
Cocos nucifera	1	0	819156	1153237
Cocos nucifera	1	0	819144	1153258
Cocos nucifera	1	0	819384	1153279
Cocos nucifera	1	0	818738	1151945
Cocos nucifera	1	0	818906	1152094
Cocos nucifera	1	0	819134	1153254
Cocos nucifera	1	0	819172	1153228
Cocos nucifera	1	0	817635	1155658
Cocos nucifera	1	0	817634	1155661
Cocos nucifera	1	0	817707	1155630
Cocos nucifera	1	0	817761	1155560
Cocos nucifera	1	0	817694	1155565
Cocos nucifera	1	0	817686	1155593
Cocos nucifera	1	0	817683	1155596
Cocos nucifera	1	0	818115	1155038
Cocos nucifera	1	0	818087	1154985
Cocos nucifera	1	0	817902	1155724
Cocos nucifera	1	0	817739	1155715
Cocos nucifera	1	0	817727	1155716
Cocos nucifera	1	0	814372	1152161
Cocos nucifera	1	0	814372	1152162
Cocos nucifera	1	0	814561	1152088
Cocos nucifera	1	0	814748	1152016
Cocos nucifera	1	0	814744	1152028
Cocos nucifera	1	0	814805	1151984
Cocos nucifera	1	0	818564	1155794
Cocos nucifera	1	0	818557	1155791
Cocos nucifera	1	0	818556	1155786
Cocos nucifera	1	0	818557	1155786
Cocos nucifera	1	0	815098	1154372
Cocos nucifera	1	0	815199	1154607
Cocos nucifera	1	0	815196	1154608
Cocos nucifera	1	0	815241	1154674
Cocos nucifera	1	0	814837	1153846
Cocos nucifera	1	0	814801	1153885
Cocos nucifera	1	0	814772	1153893
Cocos nucifera	1	0	814757	1153900
Cocos nucifera	1	0	814740	1153850

Cocos nucifera	1	0	815094	1153788
Cocos nucifera	1	0	814716	1152838
Cocos nucifera	1	0	814685	1152833
Cocos nucifera	1	0	814813	1152855
Cocos nucifera	1	0	819528	1155520
Cocos nucifera	1	0	813445	1150211
Cocos nucifera	1	0	813940	1150204
Cocos nucifera	1	0	813444	1150202
Cocos nucifera	1	0	817854	1153380
Cocos nucifera	1	0	819402	1155650
Cocos nucifera	1	0	819531	1155521
Cocos nucifera	1	0	817290	1152350
Cocos nucifera	1	0	817497	1152379
Cocos nucifera	1	0	817211	1152663
Cocos nucifera	1	0	818499	1155908
Cocos nucifera	1	0	818456	1155805
Cocos nucifera	1	0	818284	1155786
Cocos nucifera	1	0	818284	1155772
Cocos nucifera	1	0	816834	1156351
Cocos nucifera	1	0	814900	1153026
Cocos nucifera	1	0	814861	1153049
Cocos nucifera	0	0	819158	1153243

APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 3

TABLE B.1. Primer sequences and motif repeats of the 10 microsatellite loci used to genotype *Uroderma bilobatum* in Costa Rica. Primers were designed using Primer Designer (Castoe *et al.* 2010).

Primer Name and Direction	Sequence	Repeat Motif
UB_msat03_F	GCCCTCTGGTCATCACTTCC	AAC
UB_msat03_R	GCAAGGATTTATAGTTAAATGTGACAGC	
UB_msat04_F	GGTGCTTAGTGTGCTGCTGG	ACC
UB_msat04_R	CATGGAGCTGACATTTGATGG	
UB_msat21_F	AGAAGGGCTTGGAGGTTAGG	AAC
UB_msat21_R	GCCTTAGAAACAGCCTTGGG	
UB_msat30_F	GTGGAGGTAACATCTGCCCC	TCC
UB_msat30_R	ACTTCAGATGGGTGTGGTGC	
UB_msat32_F	AAATGATGGAAGCAGGGAGG	ATT
UB_msat32_R	CATTGTCTCAAGTCTATAAGAATCACCC	
UB_msat48_F	CGGCCACATAAAGACAGAGG	TGC
UB_msat48_R	AGTCTTGAGCGGTCTCACCC	
UB_msat58_F	GCTTCTTAGTCCAGGGCTGC	ATT
UB_msat58_R	CAGACACTTGGAGGTGCTGC	
UB_msat59_F	GGGCTGGATATTTCTGTGCC	ACC
UB_msat59_R	AAGGGTTTGGGGAGACTTGG	
UB_msat86_F	GTTTGCAAGCCTATTTGCCC	ATAC
UB_msat86_R	TCCAACAACCTCCATCCTGC	
UB_msat95_F	ACTTTGAACTCTTCATCTAGTAGACAGC	
UB_msat95_R	TCTTGACCATTTGGCTCTGG	AAAC

APPENDIX C. PERMISSIONS TO REPRINT PUBLISHED CHAPTERS

PERMISSION FOR CHAPTER 4

SAGOT, M., AND R. D. STEVENS. 2012. The evolution of group stability and roost lifespan: Perspectives from tent-roosting bats. Biotropica 44: 90-97.

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VITA

Maria Sagot was born in April 1981, in San José, Costa Rica to Ligia Rodríguez and Alvaro Sagot. She lived in Palmares, Alajuela, where she played baritone, trumpet, and clarinet in the youth symphonic orchestra. During her childhood and adolescence, Maria spent her free time playing basketball for her school team and practicing mountain biking. She was an active member of the local girl scouts and red cross. At age 17 she moved to San José to enroll as a biology student at Universidad de Costa Rica. During her first year, Maria worked as a research assistant at the Marine and Limnology Research Center. However, in her second year of college, she became interested in bats. Since that time, she has been involved in multiple research projects as an assistant and volunteered at the National Museum of Natural History, where she learned how to prepare and catalog mammalian specimens. In 2002 she got involved in the development of the Costa Rican bat conservation program. This program is still successfully active and has won various international conservation grants. After her graduation in 2004 Maria moved to Boston, Massachusetts, where she enrolled at Boston University to improve her English. During her time in Boston, she decided to go to the North American Symposium on Bat Research with the goal of finding a doctoral advisor. That is how she met Dr. Richard Stevens. Thus, in 2005 she joined the Department of Biological Sciences at Louisiana State University under his supervision. Here Maria conducted research on the effect of ecological and environmental factors on the social behavior of tent-roosting bats. Maria's current interests center on understanding how ecological and behavioral factors interact in speciation processes.